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SELECTION OF WINTER FOOD BY BEAVERS AT ELK ISLAND NATIONAL PARK

by

DOUGLAS L. SKINNER

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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Abstract

Five thousand eight hundred fourteen trees were examined on 239 vegetation plots at Elk Island National Park, Alberta to test three hypotheses about beaver (*Castor canadensis*) food selection: (1) beavers select certain classes of woody vegetation, (2) selection increases with increasing distance from water, and (3) preferred classes of vegetation are those with highest nutrient levels. Large, young trees were selected over other classes of aspen poplar (*Populus tremuloides*) whereas selection for balsam poplar (*P. balsamifera*) was strongest for those with a high rate of radial growth. Beavers never selected in favor of birch (*Betula papyrifera*). All classes of balsam poplar and large, fast-growing aspen were preferred by beavers while small, slow-growing aspen poplar and birch growing more than 17 m from water were avoided. No selection for specific plant species could be detected within 10 m of shore, although beyond that distance there was a tendency for selection of balsam poplar to increase with distance from water. Beavers removed crowns and some branches from trees they cut down but except for a tendency for the range of sizes of aspen poplar cuttings removed to decrease with distance from shore, there were no obvious patterns of removal. Aspen and balsam poplar were high in most nutrients before and after storage in an artificial food cache. Alder had the highest protein levels while birch was low in all nutrients analyzed. Plant species selected most frequently were those highest in most nutrients; however, within plant species, selection for high concentrations of nutrients was not evident. Other factors, such as competition from other herbivores and energetic cost:benefit ratios may influence intraspecific selection.

Beaver populations at Elk Island National Park (0.94 per km^2) are among the highest reported in Canada. A high number of animals per colony, low reproductive rates, and colonization of previously abandoned colony sites suggest that beaver habitat is saturated. Rates of regeneration of preferred classes of trees do not appear adequate for long-term support of the current population density.

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I. INTRODUCTION

Beavers (*Castor canadensis*) feed on a variety of plant material including herbaceous aquatic and terrestrial vegetation and woody vegetation. During fall, they characteristically shift from a diet of predominantly herbaceous material to the almost exclusive use of woody foods (Svendsen 1980a). Some trees cut down in fall are used immediately but others are transported to the vicinity of a lodge or bank burrow to serve as a cache of food when winter activity is restricted by ice cover. Since northern beavers are unable to forage for alternative foods in winter, it is crucial that the cache contain sufficient reserves of energy and nutrition to maintain the colony until the ice breaks up in spring.

Adult beavers defend exclusive home ranges (Brenner 1967, Aleksiuk 1968). This allows the researcher to attribute foraging patterns and food caches to specific colonies.

Beaver food preferences have been studied by many workers (Aldous 1938, Hiner 1938, Shadle *et al*. 1943, Stegeman 1954, Hall 1960, Brenner 1962, Novakowski 1967, Aleksiuk 1970, Northcott 1971, Jenkins 1975, Slough and Sadleir 1977, Jenkins 1979, Jenkins 1980). Most food habit studies have concentrated primarily on selection of species and many (Hall 1960, Northcott 1971, Slough and Sadleir 1977) have indicated that aspen poplar (*Populus tremuloides*) is used preferentially where it is available, while willow (*Salix* spp.) and alder (*Alnus* spp.) are important in the absence of aspen (Hall 1960, Novakowski 1967, Northcott 1971).

Some workers have attempted to assess the effect of tree diameter on selection. Hall (1960) indicated that willow in the 5 cm class was selected preferentially while Stegeman (1954) reported a preference for aspen 2.5 cm in diameter. Jenkins (1980) reported that the size of felled trees diminished with distance from water. Chabreck (1958) briefly examined the effect of growth rate on selection.

The nutritional regimen of foods used during winter was examined by Novakowski (1967). He assumed that small twigs were entirely consumed but subsequent studies by Aleksiuk (1970) indicated that this was not the case. Jenkins (1979) reported seasonal changes in preferred species. He postulated that they resulted from variations in nutritional stability between species of woody vegetation.

Food selection by beavers in Massachusetts was studied by Jenkins (1975, 1978, 1979, 1980). He reported that selection was affected by stem diameter in some genera

but not in others (Jenkins 1975). However, most studies of beaver food habits have concentrated mainly on selection at the plant species level. Few workers have attempted to determine (1) whether beavers select woody vegetation in particular diameter or age classes and (2) the criteria governing any such selection.

Foraging patterns of beaver in the southern boreal forest of central Alberta were examined. Specifically, the hypotheses tested were:

1. beavers select particular species, sizes, and age classes of woody vegetation for use as winter food.
2. selection of woody vegetation increases as beavers travel farther inland to obtain forage.
3. preferred classes of vegetation are those containing highest concentrations of nutrients. Since overwinter storage in water may result in the leaching of nutrients, the effects of immersion were examined.

The focus of the present study was to examine the overall foraging patterns of a large population of beavers in the southern boreal forest. Although site-specific (Jenkins 1975) and temporal (Jenkins 1979) variations in foraging have been reported, I did not examine them in the present study.

II. STUDY AREA

The study was conducted at Elk Island National Park, a fenced area occupying 194 km^2, in central Alberta, 35 km east of Edmonton (Fig. 1). The park is located in the Beaver Hills, a region of knob and kettle terrain characterized by large numbers of small lakes that provide habitat for beavers.

A four-lane highway divides the park into the Main Park to the north and the Isolation Area to the south. Major aquatic features of the Main Park are Astotin and Tawayik Lakes while Flyingshot Lake is a dominant feature of the Isolation Area.

The park is located at the southern fringe of the Mixedwood Section of the Boreal Forest Region (Rowe 1972). Aspen poplar and balsam poplar (*Populus balsamifera*), typical of upland sites and moist lowlands, respectively, are the dominant tree species. Birch (*Betula papyrifera*) occurs commonly in poplar forests or as small, pure stands. White spruce (*Picea glauca*) occurs infrequently in pure stands and occasionally in the understory of deciduous stands. However it is most common on islands in lakes. Larch (*Larix laricina*) and black spruce (*P. mariana*) are sparsely distributed.

Dominant shrubs include rose (*Rosa acicularis*), beaked hazel (*Corylus cornuta*), raspberry (*Rubus strigosus*), and saskatoon (*Amelanchier alnifolia*). Willow, red osier dogwood (*Cornus stolonifera*), and alder (*Alnus tenuifolia*) are less common. Sedge (*Carex* spp.) meadows are often associated with water bodies.

The climate is typical of the central, cool, temperate zone with cold winters and short, cool summers (Longley 1967). January is the coldest month with a mean temperature of -16°C while July, the warmest month, has a mean temperature of 17°C. Annual snowfall averages 140 cm. Ice typically covers standing water from November until May.

III. METHODS

A. Foraging Inventory

Thirty-three locations within Elk Island National Park were examined to determine beaver foraging strategies. One location was undisturbed by beavers and 2 were recently abandoned colonies, established 1 to 19 years previously and recorded as active during the April 1981 aerial survey conducted by Parks Canada. The remaining 30 had active colonies.

The colonies studied were selected because they had been occupied continuously over a number of years according to aerial survey data provided by Parks Canada. Since aerial surveys were not conducted annually, I was unable to determine the precise age of colonies and they were therefore grouped into 4 age categories (Table 1).

At each colony, plots 5 m wide, extending 30 m perpendicular from the water's edge were established at 25 m intervals along the shoreline. One plot was usually placed directly behind the beaver lodge. Generally, plots were placed on each side of the original until a plot in each direction from the lodge was established beyond the foraging range of the colony. The number of plots ranged from 3 to 14 ($x=7.2$) per colony.

At each plot, bank height and slope were measured with a clinometer. Trees and shrubs were tallied if at least one-half of the trunk was within the plot and the basal diameter was greater than 2 cm. For each tree tallied, the following information was recorded:

1. distance from open water
2. species
3. basal diameter
4. age
5. cut by beavers or not

Trees and shrubs less than 2 cm in diameter were not included because of the difficulty of distinguishing beaver from snowshoe hare (*Lepus americanus*) browsing in small size classes of shrubs. The distance of each tree from open water was measured to the nearest meter with a measuring tape oriented along the long axis of the plot. Plant

identification followed Budd (1979). Willows were identified to species unless extensive cutting precluded identification at that level. However, for analysis, all willows were included in a single category. Basal diameter was measured at a height of approximately 0.5 m and age was determined by counting annual rings from an increment bore. Ages of poplars, however, often were not determined because of decay at the center of the trunk. Trees cut down by beavers were classified as fresh (cut within the last year) or old by the coloration of the stump.

Diameters and ages of branches removed from felled trees were estimated by examining portions of them remaining on trees. The distance of terminal ends of trees from water also was recorded. Where foraging extended beyond the limit of the standard plot, the plot was extended to include it.

An inventory of 239 plots and 5814 trees was undertaken by this method. Because old cuttings were unlikely to indicate current patterns of use, they were not included in data analyses. Therefore, the data used included information on 1006 aspen poplar, 1025 balsam poplar, 1347 birch, 106 willow and 62 alder.

The location of each plot was recorded on a 1:25,000 airphoto mosaic. The mosaic was used to determine overwater distance from the lodge to each plot and the surface area of each waterbody. Because methods were changed slightly near the beginning of the study, data from three colonies sampled early were not included in data analyses.

B. Necropsies

Twenty beavers to be examined for tularemia (*Francisella tularensis*) and *Giardia* spp. were collected at Elk Island National Park from 30 April to 10 August 1982 by the Warden Service. They were weighed, measured (total length and tail length), sexed, and then necropsied to determine reproductive condition, age, composition of the stomach contents, and general health.

Reproductive rates were determined by counting embryos or placental scars. Age was determined from the amount of root closure and number of annual cementum layers in the mandibular molars (Van Nostrand and Stephenson 1964). Stomach contents were measured volumetrically. The contents were then allowed to dry and a 1.5 g subsample

was examined. Because stomach contents were thoroughly masticated, an analysis of the species composition of ingested food was not conducted; instead stomach contents were examined to determine the weight of herbaceous material, wood, and bark within the sample. If materials were present in trace amounts, they were assigned a minimum weight of 0.1 g.

C. Food Cache Composition

In October 1982, 24 food caches were sampled to determine species, ages, and diameters of constituent woody vegetation. Because access by boat to most locations sampled during the foraging inventory was poor, only 5 food caches examined were associated with those colonies. Twenty-one of the 24 food caches were on Astotin or Tawayik Lakes and the remainder were located on smaller ponds.

At each food cache, 20 samples, each consisting of a single cutting, were removed. Because Slough (1978) reported that surficial materials differed from those in the remainder of food caches, 5 samples were taken from the surface of the water and the remaining 15 from below the surface by means of a grappling hook with a 90 cm shaft. Since most caches were established in less than 1 m of water, the length of the shaft was adequate to allow sampling to the bottom of all caches. For each sample removed, species, diameter at the point of cutting, age, and location in the cache (surface or subsurface) was recorded.

D. Nutrient Analysis

In November 1982, 86 paired samples of various species, sizes, and age classes of woody vegetation were collected from areas adjacent to beaver ponds sampled during the foraging inventory. Branches of various sizes were also collected from larger trees; however, because of the difficulty of obtaining adequate volumes of material for analysis from branches of a particular tree, ages of branches were not recorded.

Bark was removed from one member of each pair and submitted to Alberta Agriculture Soil and Feed Testing Laboratory for an assessment of nutrient content. Components assayed included percent moisture, protein, calcium, phosphorus, and fibre.

The remaining member of each pair was wrapped in wire mesh, attached to a length of rope and placed in Astotin Lake to mimic the effects of storage in a winter food cache.

Sixty-two (72%) of the samples in the artificial food cache were recovered in May 1983. The loss of material was partially a result of vandalism; a rope used to moor the samples to a nearby island was removed during winter. There was also evidence that the artificial cache had been disturbed by beavers. The material recovered was subjected to the same analyses as the controls.

E. Aerial Surveys

Aerial surveys to determine the current status (active or abandoned) of colonies, as well as to locate occupied bank burrows were conducted in Elk Island National Park on 14 and 15 November 1982.

East-west transects spaced at 0.4 km intervals were flown in a Cessna 172 at an altitude of 150 m above ground level and an airspeed of 150 km per hr. Two observers seated on opposite sides of the aircraft plotted observations of beaver lodges and food caches on a 1:25,000 airphoto mosaic. Although weather conditions were good at the time of the survey, observability was considered to be only poor to fair because of light ice and snow cover which had formed a few days previously.

IV. RESULTS

A. Abundance and Distribution of Beaver Colonies

During the 1982 fall survey, the presence of food caches indicated that 182 beaver colonies were active (Fig. 1). An additional 133 abandoned lodges were recorded. Eleven (17.5%) of 63 lodges, the locations of which were known precisely from summer field studies, were not recorded from the air, an indication that actual densities exceed recorded densities. Of 30 locations checked from the ground, 1 (3.3%) was erroneously identified as active.

Seventeen (53%) of 32 colonies sampled during the summer foraging inventory were active in fall, 13 (41%) were inactive and the status of 2 (6%) not observed from the air was unknown.

Overall, the density of beaver colonies at Elk Island National Park was 0.94 colonies per km^2. The Main Park, which has an area of 129.5 km^2, contained 134 colonies (1.07 per km^2) while the Isolation Area had a density of 0.74 colonies per km^2 (48 in 64.8 km^2). Thirty-five colonies were observed on the six largest lakes in the park, although most (18) were located on Astotin Lake. The region east of Astotin Lake was also an area of high density. Other concentrations of beaver were observed along the park boundary west of Tawayik Lake and near the south park boundary.

B. Effects of Major Habitat Features

Major habitat features used in the following analyses were mean and maximum browsing distance from water; mean overwater distance to foraging areas; mean bank height; mean bank slope; surface area of the water body; total basal area (cm^2 of stem per m^2 of ground); density of woody stems (stems per m^2); basal area and mean diameters of aspen poplar, balsam poplar, birch, and other species available within 30 m of water. Variables were tested for skewness and kurtosis and where necessary transformed.

Effects on Colony Abandonment and Age

A discriminant function analysis was used to compare habitat features of colonies that were active in fall 1982 with those that were inactive. None of the variables entered into the analysis had sufficient discriminating power to differentiate between the two groups ($p>0.05$). The results were similar when active and inactive age class 1 (less than 3 yr old) colonies were compared ($p>0.05$), which suggests that areas supporting active beaver colonies are similar in habitat characteristics to areas that have been abandoned.

Similarly, a discriminant function analysis indicated that no significant differences existed among habitats occupied by different age classes of beaver colonies ($p>0.05$).

Effect on Foraging Patterns

At each colony, mean and maximum foraging distance from shore was determined. These were used as dependent variables in stepwise multiple regression analyses with major habitat features as independent variables.

Mean and maximum foraging distances were highly correlated ($r=0.90$), and the factors explaining them were similar (Table 2). However the regression equation for mean distance explained more of the variance ($r^2=0.80$) than the equation for maximum foraging distance ($r^2=0.57$). For both dependent variables, total basal area, a measure of the total amount of timber available within 30 m of water, had the greatest explanatory power. It explained 59% and 41% of the variance in mean distance and maximum distance, respectively. Basal area of birch explained 14% of the variance in both dependent variables. Both total basal area and the basal area of birch were negatively correlated with foraging distance, which indicates that beavers browsed farther inland in areas of low timber availability. Stem density of shrubs was positively associated with mean foraging distance although the association was weak. This may result from the increased density of shade intolerant shrubs as the overstory of timber is depleted.

C. Selection of Woody Vegetation

To examine patterns of selection, foraging was examined for each age class of beaver colony at four distance intervals: (1) 0 to 10 m from shore, (2) 11 to 20 m, (3) 21 to 30 m, and (4) more than 30 m from shore.

Within each distance interval, selection at the species level was tested (G-test) for goodness of fit. If departures from expected values were significant ($p<0.05$), selection for each species was tested (G-test) for independence. The strength of selection was determined by calculating the forage ratio as modified by Jacobs (1974). The forage ratio measures selection from negative infinity to positive infinity and has the advantage of a symmetrical distribution. When the frequency of cutting did not depart significantly from expected values, species comprising less than one percent of the sample were dropped from the analysis. Silverberry (*Eleagnus commutata*), although comprising 1.3% of the vegetative samples, was found at a single beaver colony and was therefore also excluded from further analysis.

A two-way analysis of variance was used to compare the basal diameter of cut and uncut trees of each species at each distance interval. Prior to these analyses, the variances of cells in the model were compared by means of Bartlett's test of homogeneity of variances (Sokal and Rohlf 1981). Where variances were significantly different, the data were transformed.

The relationship of the age of various tree species with cutting, basal diameter, and distance from open water was examined by means of a series of stepwise multiple regressions (Kleinbaum and Kupper 1978). Age (dependent variable) was regressed on diameter, distance from open water, the dummy variable cut, and the interaction terms, cut multiplied by diameter and cut multiplied by distance in the model:

$$Y(age) = B_0 + B_1(dia) + B_2(dist) + B_3(cut) + B_4(dia \times cut) + B_5(dist \times cut)$$

If interaction was significant, indicating difference in slope, the equation was partitioned into two regression equations, one for cut and the other for uncut trees. If the interaction terms were insignificant, significance in the dummy variable, cut, indicated a difference in intercept. An analysis of covariance (ANOCOVA) was then used to detect

differences in age between cut and uncut trees.

Shrubs

Willow and alder were the only shrubs retained for data analysis. Statistically, there was little selection for or against alder, since its use was always proportional to its frequency of occurrence.

Because of its sparse distribution, its use was not broken down by colony age class or distance from open water. The diameter of uncut alder ($x=6.6$ cm) did not differ significantly from the mean of 5.7 cm for those cut down by beavers ($t=0.734$, $p=0.45$). Similarly a multiple regression analysis indicated no difference in ages of cut and uncut alder ($F=1.008$, $p=0.32$).

Willow was used preferentially only at age class 1 colonies. At distances of 11 to 20 m from water, a forage ratio (FR) of 1.552 indicated strong selection for that genus ($G=18.915$, $p=0.000$). However, selection for certain diameter ($t=0.898$, $p=0.40$) and age-classes ($F=0.014$, $p=0.91$) was not evident.

There was a strong tendency for the use of willow and alder to decrease as colony age increased ($G=13.448$, $p=0.001$). At age class 1 colonies, beavers cut 35.8% (24 of 67) of the willow and alder available. This decreased to 6.3% (4 of 63), 4.2% (1 of 24), and 0% (0 of 22) at age classes 2, 3, and 4 respectively.

To determine if this pattern indicated selection for willow and alder or selection for diameter classes characteristic of those species, a 99% confidence interval was constructed around the mean diameter of cut shrubs ($3.7 \leq x \leq 6.7$). The frequency of use of aspen poplar, balsam poplar, and birch within this range of diameters was then compared among the four colony age classes. Use of this diameter class in these species, which ranged from 9.3% to 13.8% of the trees available ($G=2.485$, $p=0.35$), remained fairly constant among colony age classes. The strong selection for willow in young colonies and the tendency for the use of shrubs to decrease with increasing colony age therefore appears to represent selection at the species level rather than selection for specific size classes of vegetation.

Aspen Poplar

In general, beavers used aspen poplar in proportion to its availability in habitats adjacent to beaver colonies. Beavers in colony age classes 1 and 3 neither preferred nor avoided aspen (Table 3). A forage ratio of 0.709 indicated that beavers in age class 2 colonies preferred aspen poplar growing 11 to 20 m from water while strongly avoiding that species when more than 30 m from shore (FR=-1.168). Beavers in age class 4 colonies selected very strongly against aspen poplar growing 11 to 20 m from water (FR=-2.295) but selection was neutral at all other distances.

At all except age class 4 colonies, basal diameter of aspen poplar varied with distance from water and at all colonies, those cut down were significantly larger than those left standing ($p<0.05$). However, two-way ANOVAs indicated that the two effects were not interrelated (Fig. 2). The difference in diameter was greatest in age class 2 colonies (x cut=24.5, x uncut=13.7) and smallest in age class 3 colonies (x cut=24.9, x uncut=19.2). This may result from class 3 colonies having aspen of the greatest average diameter of any age class. Aspen of small diameter characterized sites occupied by class 1 and 4 colonies, which resulted in beavers cutting down relatively small size classes. In class 1 colonies, the average diameter of cut trees was 19.0 cm (x uncut=12.4) while in class 4 colonies it was 19.3 cm (x uncut=10.5). There is a slight tendency for the difference between diameters of cut and uncut aspen to increase with distance from water in young colonies (classes 1 and 2) and to decrease with distance in old colonies.

In class 1, 2, and 4 colonies, ages of trees cut down by beavers and those left standing differed significantly for any given diameter (Table 4). The difference tended to increase with increasing basal diameter. In age class 1 colonies, cut and uncut trees 2 cm in diameter were approximately nine years old. In the 20 cm class, uncut trees averaged four years older than trees of the same size felled by beavers. The age of aspen poplar in class 2 colonies was affected by distance from water. Age in both cut and uncut trees decreased an average of 0.18 years for each meter increase in distance from water. Uncut aspen poplars 2 cm in diameter were approximately 0.5 years older than cut trees of the same diameter whereas uncut 20 cm trees were approximately 5 years older than cut trees of the same diameter. The age of aspen poplar in age class 4 colonies was also

dependent on distance from shore. However in this case, age increased 0.30 years for each additional meter from water. Age class 4 colonies exhibited the greatest difference between the ages of trees felled by beavers and those left standing. In the 2 cm class, standing trees were about 1 year older than felled trees while in the 20 cm class this difference increased to 9.5 years.

Therefore, where aspen poplar is concerned, there is little evidence that foraging patterns differ because of colony age or distance from shore. In all age classes, beavers tended to fell the largest trees available and select the youngest trees in any diameter class.

Balsam Poplar

The use of balsam poplar by beavers ranged from neutral to strong preference (Table 3). In no colony age class, did beavers select at the species level at distances less than 10 m from water. In classes 1, 2, and 4 the forage ratio indicated that the strength of selection in favor of balsam poplar increased with increasing distance from water. No selection for balsam poplar at age class 3 colonies was evident.

The relationship between the basal diameter of balsam poplars felled by beavers and those left standing did not vary consistently with colony age (Fig. 3). At class 1 colonies, a two-way ANOVA indicated that the diameter of cut balsam poplar was significantly greater than that of uncut ($\bar{x}$ cut=19.2, $\bar{x}$ uncut=13.5). However the relationship did not vary significantly with distance from shore. In class 2 and 3 colonies, the relationship between diameter of cut and uncut trees depended on distance from water. In class 2 colonies, the diameter of cut trees ($\bar{x}$=26.9) was slightly greater than that of uncut trees ($\bar{x}$=22.8) less than 10 m from water whereas at distances of 11 to 20 m, standing balsam poplar trees ($\bar{x}$=17.8) were considerably larger than trees cut down by beavers ($\bar{x}$=10.7). At distances greater than 20 m, cut and uncut trees had similar diameters. Conversely, in age class 3 colonies, beavers cut down trees ($\bar{x}$=27.3) much larger than those they left standing ($\bar{x}$=19.1) 11 to 20 m from shore. At other distances the diameter of both groups was similar.

Because none of the transformations stabilized cell variance, no two-way ANOVA was calculated for age class 4 colonies. Instead, a Kruskal-Wallis test was used to

explore the relationship between basal diameter and distance from shore. At each distance interval, a Mann-Whitney U test was used to determine whether diameters of felled and standing balsam poplar were significantly different.

The Kruskal-Wallis test indicated that the diameter of balsam poplar, which ranged from an average of 13.1 cm at distances of 21 to 30 m to 17.7 cm at greater than 30 m, varied significantly with distance from water. However, diameters of trees felled by beavers did not differ significantly from those of standing trees at any distance from shore. Nevertheless, there was a slight tendency for cut trees to decrease in size relative to standing trees as distance from water increased (Fig. 3). Near water, the mean diameter of trees cut down was 19.0 cm compared to an average of 15.7 cm for uncut trees. (U_1=799.5, U_2=1234.5, p=0.141) whereas at distances of 21 to 30 m, cut trees tended to be smaller than those left standing ($\bar{x}$ cut=9.3, $\bar{x}$ uncut=13.4, U_1=195.5, U_2=231.5, p=0.083).

Selection for ages of balsam poplar appeared to be related to the use of diameter classes. In age classes 1 and 3, where the size of cut trees generally exceeded that of uncut trees, there was little selection for age (Table 5). However, in classes 2 and 4, where standing trees tended to be larger, felled trees of any given diameter were younger than standing trees of the same diameter. In class 2 colonies, trees cut down by beavers were an average of 3.4 years younger than uncut trees of equal diameter (ANOCOVA) while at class 4 colonies the difference in age increased with increasing diameter. Balsam poplar 2 cm in diameter cut by beavers was an average of 0.5 years younger than uncut 2 cm balsam poplar whereas cut 20 cm trees were approximately 4.6 years younger than uncut trees of the same diameter.

Except for a tendency for beavers to select more strongly in favor of balsam poplar as distance from shore increased, there were no evident patterns of selection that could be related to distance from shore or colony age. Selection for diameter and age was related, with beavers selecting in favor of young trees where those of small diameter were taken.

Birch

Beavers always either used birch in proportion to its availability or selected against it (Table 3). In all colony age classes, the use of birch was proportional to its availability within 10 m of shore. Beavers in class 1 and 2 colonies strongly avoided birch beyond that distance while in older colonies (classes 3 and 4), avoidance was not evident up to 21 m from the water's edge.

There is little indication of a consistent pattern of selection based on tree diameter. The ANOVAs indicated that in class 1 and 4 colonies, the relationship between cut and standing trees varied with distance from shore (Fig. 4), although the patterns were different. In age class 1 colonies, diameters of cut and uncut trees were similar from 0 to 10 m from water. Between 11 and 20 m, the mean diameter (10.9 cm) of trees felled by beavers greatly exceeded the mean (3.0 cm) of those left standing. This difference declined beyond 20 m, although the diameter of cut birch ($\bar{x}$=7.5) was still substantially greater than that of those not cut ($\bar{x}$=3.5). In class 4 colonies, the diameter of birch used by beavers ($\bar{x}$=3.5) was smaller than that of uncut birch ($\bar{x}$=6.5) near the water, approximately the same at 11 to 20 m, and larger ($\bar{x}$ cut=6.6, $\bar{x}$ uncut=4.9) beyond 20 m. In the remaining colony age classes, the diameter of cut and uncut trees was not significantly different.

Selection for diameter class was associated with selection for age in birch trees. In class 2 and 3 colonies, there was no evident selection for either diameter or age classes of birch. However, in class 1 and 4 colonies younger trees were selected (Table 6). In class 1 colonies, the age difference between trees cut down and uncut trees varied with diameter; cut trees 2 cm in diameter were an average of 2.8 years older than uncut trees of the same size, while standing birch 10 cm in diameter was about 4.8 years older than cut 10 cm birch. At class 4 colonies, cut birch 2 cm in diameter was 4.2 years younger than those left standing while in the 10 cm class, cut trees were about one year older than uncut trees.

Overall patterns of selection

In the three trees species considered, selection for age was associated with selection for diameter. Large diameter and young age characterized aspen poplar cut down by beavers. For balsam poplar, selection for age was not evident where beavers cut down large trees; where cut trees were small, beavers tended to use young trees in any diameter class. Selection for age in birch was also associated with selection for size, although in this case, young trees were selected where there was selection for certain diameter classes. Overall, balsam poplar was most strongly selected while birch was avoided. The use of aspen poplar generally reflected its availability.

However, except for a tendency for beavers to become more selective for balsam poplar as distance from water increased and the absence of selection at the plant species level within 10 m of water, there were no obvious patterns of selection that could be related to colony age or distance from shore. Therefore, all colony age classes were combined in the remaining analyses.

The relationship between the proportion of trees cut down in each one meter interval and distance from water for the three principal tree species was explored with stepwise polynomial regressions. Proportions were transformed by the angular method.

The regression equations indicated that cutting patterns in aspen and balsam poplar were similar while those of birch were somewhat different (Fig 5). The equation for aspen poplar provided a moderate explanation of the distribution of the data (r^2=0.39). In general, the proportion of cut trees remained constant at about 32% over the 8 m nearest the water and thereafter declined, reaching 0% at 33 m. The equation for balsam poplar explained only 20% of the variance (r^2=0.20). It indicated that about 29% of the available balsam poplar are cut down by beavers in the first 16 m. After 16 m, the proportion of trees cut down declines rapidly to 0% at 33 m. Distance from water explained 65% of the proportion of birch used by beavers (r^2=0.65). In this case, 50% of the trees available near the water were cut down. The proportion of cut trees declined rapidly with distance, reaching 0% at 29 m.

To determine how beavers selected among classes of woody vegetation, the variables diameter, age, growth rate, and distance from shore were entered into a discriminant function analysis to identify characteristics of cut and uncut trees. Significant

variables were then used to classify trees into groups which were tested to determine if the frequency of cutting was proportional to the frequency of occurrence. Forage ratios were calculated where significant departures from randomness occurred.

The discriminant function analysis indicated that age and basal diameter were the best discriminators of cut and uncut aspen poplar (Table 7). Beavers tended to cut down trees that were both large and young. On the basis of those variables, the analysis correctly classified 70.6% of cut and uncut aspen poplar. The only discriminating variable derived for balsam poplar was growth rate, which was greater for cut than uncut trees. However, the ability of the function to classify balsam poplar correctly was weak (59.0% correctly classified). The significant discriminating variables for birch were growth rate and distance from water. Again, beavers tended to cut down fast-growing trees and those they cut were closer to water than those they left standing. These variables correctly classified 74.1% of cut and uncut birch.

Trees were generally separated into categories based on the discriminating variables derived from the analysis. However, because of the large diameter of felled aspen poplar, very few trees could be classified as both large and young. Therefore, since previous analyses showed that beavers cut down the fastest-growing trees in any diameter class, growth rate instead of age was used to separate aspen poplar into groups. The midpoint between the mean of cut and uncut trees was used as the point of separation. Therefore, four classes of aspen poplar were recognized:

1. basal diameter greater than 15 cm and annual growth less than 0.39 cm.
2. basal diameter greater than 15 cm and annual growth 0.39 cm or more.
3. basal diameter less than 15 cm and annual growth less than 0.39 cm.
4. basal diameter less than 15 cm and annual growth 0.39 cm or more.

Similarly, four classes of birch were recognized:

1. annual growth less than 0.30 cm and distance from water 17 m or less.
2. annual growth less than 0.30 cm and distance from water greater than 17 m.
3. annual growth 0.30 cm or more and distance from water 17 m or less.
4. annual growth 0.30 cm or more and distance from water more than 17 m.

In balsam poplar only two classes were recognized; those with annual growth of more than 0.42 cm and those with annual growth of less than 0.42 cm.

The forage ratio indicated that beavers preferred three classes of trees (Fig. 6). Fast-growing balsam poplar (G=87.086, p=0.000, FR=0.938) had the highest preference rating followed by large, fast-growing aspen poplar (G=16.481, p=0.000, FR=0.616) and slow-growing balsam poplar (G=18.236, p=0.000, FR=0.432). An additional three classes were avoided by beavers. Slow-growing birch, more than 17 m from water was avoided most strongly (G=124.394, p=0.000, FR=-2.020) followed by fast-growing birch at the same distance (G=39.411, p=0.000, FR=-1.235). Beavers also selected against small diameter, slow-growing aspen poplar (G=22.183, p=0.000, FR=-0.845). Selection for the remaining four classes was not statistically significant ($p>0.05$).

Since basal diameter appears to be an important factor in the selection of aspen poplar, the effect of the relative diameter of aspen and balsam poplar on selection was tested by means of a Spearman's rank order coefficient. Because there was no selection for species within 10 m of water and beavers cut down few trees more than 30 m from water, those distance intervals were omitted from the analysis. The results indicated that selection for balsam over aspen poplar was weak where basal diameters of aspen were greater than those of balsam poplar. Where aspen poplars were smaller than balsam, balsam poplar was selected preferentially ($r=0.87$, $p=0.010$).

A similar test was performed to determine if relative selection for aspen and balsam poplar was affected by the relative density of the two species. With all colony age classes and the previous distance intervals included, the relationship between selection and relative density of aspen and balsam poplar was weak ($r=0.18$). However, if three areas where basal diameter of aspen poplar greatly exceeded that of balsam poplar are excluded from the analysis, the correlation between relative density and relative selection increases dramatically ($r=0.98$, $p=0.060$). The strength of selection for the two species is most similar where densities are almost equal and increases in favor of balsam poplar as density of balsam poplar increases in relation to that of aspen poplar.

It therefore appears that relative diameter and relative density were two major factors governing the selection of aspen and balsam poplar by beavers. Although balsam poplar was almost always the principal species selected, the availability of large diameter aspen poplar weakened the strength of this selection. The second factor, relative density, does not appear to exert much effect on selection where the diameter of aspen was

greater than that of balsam poplar. In remaining areas, selection for balsam poplar over aspen poplar depended on their relative abundances.

D. Use of Cuttings

Although large trees felled by beaver were usually not entirely removed from cutting sites, bark on the trunk was often eaten and branches were removed. Balsam poplar was the principal material removed from cutting sites by beavers, constituting 48.6% (500) of all freshly-cut removals while aspen poplar was second with 37.3% (383). Birch, alder, and willow represented 9.9% (102), 1.6% (16), and 1.4% (14) respectively. Other shrub species made up 1.3% (13) of the material removed by beavers.

Patterns of Removal

Patterns of removal were examined for aspen and balsam poplar. Other woody plant species were not included since most were of small enough diameter that entire plants were removed; for example, 98 of 102 (96.1%) birch trees were completely removed from cutting sites. Therefore patterns of removal were very similar to patterns of selection in species other than aspen and balsam poplar.

Beavers generally removed the crown and some branches from large trees they felled. The crown represented the largest part removed from the site and was usually cut where the diameter of the trunk was about 13 cm. Any branches removed tended to be much smaller and averaged 4.6 and 4.9 cm in diameter in aspen and balsam poplar, respectively. The relationship of each of these two categories of material with distance from water was examined separately and in combination with that of trees which had been entirely removed to determine if an overall pattern of removal existed.

Stepwise polynomial regressions were used to explore the relationship of diameter, age, and growth rate (cm/yr) to distance from water for material which had been removed from shore by beavers. Similar analyses were conducted on the variance of diameters, ages, and growth rates at each one meter interval from shore to determine if the ranges over which they were selected varied with distance from water. The results are reported only if $p<0.05$ and $r^2>0.10$.

The regression analyses indicated that, in general, there was little relationship between distance from open water and pattern of removal. Only the regression including the variance in diameter of all aspen poplar removed from cutting sites was significant. It indicated that there was a tendency for the size range of these materials to decrease exponentially with distance (Fig. 7). It therefore appears that while the mean diameter of aspen poplar removed by beavers does not vary substantially with distance from water, there is a tendency for beavers to select more specifically for certain diameter classes as distance from water increases.

Disposition of Cuttings

Woody materials cut by beavers can be used either in construction of dams and lodges or as a source of food. At Elk Island National Park, many waterbodies occupied by beavers have not been dammed and construction materials are used principally for lodge contruction. Recently constructed beaver lodges were smaller than old lodges and consisted mainly of unpeeled woody material about 3 cm in diameter. The material used for construction appeared to reflect the occurrence of species of that size on the shore adjacent to new beaver lodges. Older lodges were made primarily of wood from which bark had been peeled, likely remains of previous food caches. Overall, barked wood was the most important construction material. Of 227 pieces of wood collected randomly from 11 lodges, 170 (74.9%) were barked, while unpeeled material consisted of 21 poplar (9.3%), 14 willow (6.2%), 13 birch (5.7%), and 6 alder (2.6%). Three items (1.3%) consisted of other woody plant species. Since bark is used as food, the high proportion of peeled wood found in lodges indicates that woody material was selected primarily as winter food.

Surveys of 24 winter food caches indicated that the species composition and diameter of woody vegetation in food caches did not accurately reflect those of cuttings observed during the foraging inventory (Table 8). Some of the difference was a result of not collecting data on material less than 2 cm in diameter during the foraging inventory but even if only food cache items 2 cm in diameter or greater are considered, the size of materials found in food caches is smaller than that of cuttings observed along the shore. The difference is greatest for balsam poplar where the average size removed from shore

(x=7.4 cm) is almost twice as large as that found in food caches (x=3.8, t=11.675, p=0.000). Similarly, birch removed from shore averaged 5.9 cm at the point of cutting whereas in food caches the average diameter was 4.5 cm (t=2.607, p=0.010). Alder removed from shore (x=5.8 cm) was also larger than that found in food caches (x=4.0, t=2.005, p=0.052). The diameter of both aspen poplar (t=1.348, p=0.19) and willow (t=0.587, p=0.57) was about the same for cuttings on shore and those in food caches.

Slough (1978) noted that the species composition of surficial materials differed from that in the remainder of food caches. At Elk Island National Park, species composition and size of woody material varied with layer. Balsam poplar was found primarily in subsurface layers where it constituted 33% compared with 23% of surface layers (G=3.337, p=0.072). The average diameter of 5.2 cm for balsam poplar in surface layers was significantly greater than the 2.9 cm diameter of subsurface balsam poplar (t=3.216, p=0.007). Similarly, hazel, which made up 12% of subsurface layers and 4% of surface layers, was principally a subsurface constituent of food caches (G=5.165, p=0.024).

Peeled wood was the predominant material in surface layers of food caches. It accounted for 25% of surface layers and only 8% of subsurface layers (G=12.521, p=0.000). Alder was typically a surficial material (19% surface and 7% subsurface; G=9.703, p=0.003) and tended to be larger on the surface (x=4.2 cm) than in the remainder of food caches (x=2.6 cm, t=1.933, p=0.066). Dogwood also occurred significantly more often (9%) on surface than in subsurface layers (3%, G=5.882, p=0.018).

Aspen poplar, willow, birch, and rose occurred in approximately equal proportions throughout food caches. However, except for rose, items at the surface tended to be larger in diameter than those in subsurface layers. These differences were statistically significant for willow (x surf=3.7 cm, x subs=2.5 cm, t=2.391, p=0.002) and birch (x surf=5.3 cm, x subs=3.2 cm, t=2.557, p=0.015). For aspen poplar, the difference (x surf=6.5 cm, x subs=4.6 cm) was substantial, although statistically insignificant (t=1.893, p=0.066).

Importance of Food Cache Materials

Novakowski (1967) reported that beavers completely consumed twigs less than 2.5 cm in diameter but Aleksiuk (1970) indicated that wood was not eaten by beavers. At Elk Island National Park, wood is consumed only in small amounts.

During field studies, 39 locations where beavers had fed were examined to determine the minimum diameter of peeled twigs. Peeled twigs less than 2.5 cm in diameter were found at 37 feeding areas with minimum diameters of 2 mm observed. A survey of growing twigs indicated that the minimum diameter for a live branch is 2 to 3 mm which strongly suggests that beaver do not intentionally consume even small twigs.

Contents of beaver stomachs were examined to determine the proportion of bark and wood ingested (Table 9). Although materials such as graminoids and leaves were the principal components of stomach contents, bark made up 17% of the contents, almost three times the 6% of wood ($t=2.341$, $p=0.033$). Wood accounted for a maximum of 20% of the stomach contents, which indicates that its ingestion is largely accidental and occurs while cutting down trees or feeding on bark and leaves. Conversely, bark constituted up to 81% of the stomach contents indicating that it is used as food.

To determine the relative importance of food cache materials, each item was assumed to be an open-ended cylinder 1 m in length with a diameter equal to the diameter at the point of cutting. The total surface area of each species was then estimated as an indicator of the amount of bark provided by each plant species. This method conservatively estimates the importance of large items, which often are longer than 1 m in length and usually have auxiliary branchlets, and liberally estimates small items less than 1 m in length.

This procedure indicated that, in terms of food stored in food caches, balsam poplar, which provided about 33% of the available bark, was the most important plant species. It was followed by aspen poplar with 23%. Willow, birch, and alder made up 14%, 13%, and 10%, respectively. Although hazel represented 10% of the items in food caches, it provided only about 4% of the available bark. Other plant species provided about 3% of the total bark.

E. Nutrient Composition of Woody Vegetation

Alberta Agriculture Soil and Feed Testing Laboratories presented results of the nutrient analysis as percent composition by weight. The results indicated that the percentage of fibre increased substantially after overwinter immersion in water. Since fibre content is unlikely to be altered by this treatment (M. Micko pers com), the change probably resulted from leaching of water-soluble compounds from samples. Thus, nutrient concentrations in spring samples represented the fraction of material that remained after leaching. Therefore, using fibre as a reference point, nutrient concentrations were recalculated to determine the amount of fall sample that remained by spring.

The amount of material not analyzed (unspecified) was calculated by subtracting assayed components from 100 g of fall sample and standardizing for the spring sample. Water content of spring samples was high as a result of lake water replacing other components. Therefore, estimates of loss of material from leaching assumed that a standardized fraction of the original moisture content remained. Because results are expressed as a proportion of a 100 g sample, data were transformed by the angular method.

Nutrient Composition of Typical Food Cache Materials

To compare nutrient composition between species of forage, all items between 2 and 5 cm in diameter, a size range typical of that found in food caches, were entered into an analysis of variance. Each component was examined both before and after overwinter immersion in water. Significant ($p<0.05$) analyses of variance were tested with Scheffe's method to locate specific differences.

Protein

An analysis of variance ($F=4.55$, $p=0.003$) indicated significant differences in fall protein content among species (Fig. 8). Alder, which had the highest protein content (6.5 g/ 100 g sample), had significantly higher levels than aspen poplar (4.8 g), balsam poplar (4.7 g), and birch (4.1 g). Beaked willow (*Salix bebbiana*) and diamond willow (*S. discolor*) were second in protein content.

By spring, beaked willow (3.5 g) and diamond willow (2.6 g) ranked fifth and sixth, repectively, in protein content (ANOVA F=2.81, p=0.028), significantly lower than alder (4.9 g) and aspen poplar (4.6 g). Aspen poplar and balsam poplar, which had ranked fourth and fifth in protein during fall, had risen to second and third, respectively, by spring.

Calcium

Fall levels of calcium were significantly lower in birch (0.53 g) than in other species (F=13.20, p=0.000). Balsam poplar (1.58 g) and aspen poplar (1.36 g) tended to have greater concentrations of calcium than willow and alder (p>0.05). By spring, calcium content in all species had declined substantially. Balsam poplar (1.34 g) retained the most calcium, followed by aspen poplar (0.98 g). However, only the difference between birch (0.62 g) and balsam poplar was statistically significant (F=3.25, p=0.015).

Phosphorus

Phosphorus levels did not differ significantly among species during fall (F=1.05, p=0.42) or spring (F=2.26, p=0.069). The highest fall levels of phosphorus (0.091 g) were found in balsam poplar and beaked willow. In spring, the phosphorus content of balsam poplar (0.056 g) remained highest of the six species analyzed while aspen poplar (0.054 g) rose from fifth to second. Beaked willow and diamond willow dropped from first and third to third and sixth repectively.

Unspecified

During fall, birch had significantly less unspecified material (34.0 g) than other species (F=50.44, p=0.000). Conversely, aspen poplar (60.6 g) and balsam poplar (58.6 g) had significantly greater amounts of unspecified material than other species with the exception of diamond willow (55.9 g) which ranked third.

By spring, balsam poplar (40.8 g) had significantly more unspecified material than any species other than aspen poplar (37.2 g). Levels of unspecified material in aspen poplar differed significantly from those of beaked willow (30.9 g), birch (30.4 g), and diamond willow (26.6 g), which ranked sixth ($F=12.00$, $p=0.000$). Alder (34.3 g) contained significantly greater amounts of unspecified material than diamond willow.

Fibre

The concentration of fibre (Fig. 9) was significantly higher for birch (57.2 g) than any other species ($F=57.88$, $p=0.000$) while aspen poplar (28.2 g) was significantly lower in fibre than any species except balsam poplar (30.6 g). Fibre contents of alder (37.8 g) and beaked willow (34.4 g) were significantly greater than that of balsam poplar.

Leaching

Leaching was significantly lower for birch (3.6 g) than for any other species ($F=18.66$, $p=0.000$). Balsam poplar (17.0 g) had the second lowest rate of leaching while diamond willow (30.1 g) had the highest.

Relative importance of woody plant species

A logical foraging strategy may be to attempt to maximize the amounts of protein, calcium, and phosphorus in food caches while minimizing the rate of leaching and amount of fibre. In such a strategy, balsam poplar appears to be a superior food cache material (Table 10). In both fall and spring, it ranked among the top two for all nutrients except protein. It also had the second lowest rate of leaching and fibre content. Similarly, aspen poplar ranked high in calcium content during fall and spring. In fall, it was relatively low in protein and phosphorus but by spring, ranked second in those nutrients. Aspen poplar had the lowest fibre content of any species analyzed, but was characterized by a high rate of leaching.

Willows were high in protein and contained moderate amounts of most other nutrients during fall but high leaching rates resulted in low levels of most nutrients by spring. In particular, diamond willow, which had the highest leaching rate, had the lowest concentrations of protein and phosphorus by spring.

Birch had a lower rate of leaching than any species examined; however, in fall, it had very low levels of nutrients and had the highest concentration of fibre. By spring, nutrient levels had risen slightly relative to other species but remained among the lowest observed. Alder, which was characterized by the greatest protein content both before and after immersion in water, contained moderate amounts of most other nutrients.

Factors Affecting Nutrient Composition

Characteristics of individual plants from which bark samples were taken were used to assess factors affecting nutrient levels within a species. Characteristics entered into the analyses included:

1. Distance of the tree from water.
2. Diameter of the main tree trunk.
3. Age of the main tree trunk.
4. Growth rate of the main tree trunk.
5. Diameter of the branch sampled.
6. Whether immersed in water or not.

The relationships of these characteristics to nutrient levels in the main tree trunk were also examined. Since the diameter of willow entered into the analysis ranged only from 2 to 5 cm, diameters of the main trunk and branches were not included in analyses for that genus.

Stepwise multiple regression analysis was used to determine the effect of plant characteristics on nutrient levels. Plant characteristics were included in analyses only if $p<0.05$. Generally, plant characteristics provided a good explanation of the nutrient content.

Aspen Poplar

The independent variables explained between 62% and 91% of the variance in nutrient concentrations but were not significantly associated with the amount of leaching or fibre content in aspen poplar branches. They also accounted for 55% and 91% of the phosphorus and fibre levels, respectively, in trunks.

Distance of the tree from water appeared to have the greatest association with the nutrient regimen of aspen poplar. This variable was directly related to protein and calcium concentrations in branches and explained 14% ($F=5.02$, $p=0.008$, $r^2=0.14$) and 32% ($F=3.96$, $p=0.021$, $r^2=0.32$), respectively, of the variance in the two. It was also negatively associated with fibre content of the trunk and explained 70% of the variance in that variable ($F=20.61$, $p=0.005$, $r^2=0.70$).

Diameter of the trunk was the major factor affecting protein content of branches ($F=58.37$, $p=0.000$, $r^2=0.56$). It also exerted a considerable effect on phosphorus levels in branches ($F=32.49$, $p=0.000$, $r^2=0.28$). In both cases, the tendency was for nutrient content to decrease as diameter increased.

A third factor, branch diameter, was weakly and negatively associated with protein ($F=5.38$, $p=0.006$, $r^2=0.05$), calcium ($F=8.24$, $p=0.001$, $r^2=0.11$), and phosphorus levels ($F=5.62$, $p=0.014$, $r^2=0.06$). The age of the trunk was positively associated with its fibre content ($F=12.53$, $p=0.012$, $r^2=0.22$). Levels of protein, calcium, phosphorus, and unspecified material in branches and levels of phosphorus in branches and trunks of aspen declined significantly after overwinter immersion in water ($p<0.05$).

Balsam Poplar

Independent variables explained from 45% to 95% of the variance in nutrient composition of balsam poplar branches. As well, they accounted for 65% of the variance in fibre content and 98% of the variance in the amount of leached material.

The age of the trunk was the principal factor influencing most of the criteria examined. Increasing the age of trunks resulted in lower protein ($F=28.41$, $p=0.000$, $r^2=0.64$), calcium ($F=18.92$, $p=0.000$, $r^2=0.52$), and phosphorus levels ($F=24.60$,

$p=0.000$, $r^2=0.41$) and higher levels of unspecified material ($F=6.35$, $p=0.010$, $r^2=0.23$) in branches. Protein ($F=25.30$, $p=0.001$, $r^2=0.71$) and phosphorus content ($F=54.91$, $p=0.000$, $r^2=0.68$) of trunks were negatively associated with their age while amounts of calcium ($F=6.71$, $p=0.024$, $r^2=0.29$) and fibre ($F=13.99$, $p=0.006$, $r^2=0.63$) were positively associated.

Distance from water was also an important factor. It was positively associated with calcium levels in branches ($F=92.93$, $p=0.000$, $r^2=0.26$) and trunks ($F=13.22$, $p=0.005$, $r^2=0.40$) and negatively associated with the fibre content of branches ($F=4.33$, $p=0.024$, $r^2=0.11$). However, growth rate had the greatest association with levels of fibre in branches ($F=12.89$, $p=0.001$, $r^2=0.40$) and a significant association with the amount of calcium ($F=15.92$, $p=0.000$, $r^2=0.17$); the tendency was for fibre content to increase and calcium to decrease as growth rate increased. The concentration of fibre ($F=8.64$, $p=0.002$, $r^2=0.14$) and calcium in branches ($F=12.75$, $p=0.001$, $r^2=0.06$) had a slight positive relationship with their diameter. Branch diameter was closely associated with the amount of material leached from samples and explained 98% ($F=154.50$, $p=0.000$, $r^2=0.98$) of the variance in leached material; leaching increased with decreasing branch diameter.

Nutrient concentrations in balsam poplar appeared to be less influenced by winter immersion than those of aspen poplar. For balsam poplar, only amounts of unspecified material in branches, protein in tree trunks, and phosphorus in branches and trunks decreased significantly after storage in a winter food cache ($p<0.05$).

Willow

Except for calcium concentration in diamond willow, immersion in water caused significant declines in levels of all nutrients in both willows. Calcium was the only nutrient associated with other factors. In beaked willow, calcium tended to increase as age increased ($F=14.52$, $p=0.003$, $r^2=0.47$), while in diamond willow, it was positively associated with distance from shore ($F=9.06$, $p=0.031$, $r^2=0.64$). Similarly, fibre levels in the latter species were highest when distance from water was high ($F=7.67$, $p=0.042$, $r^2=0.60$).

Alder

The diameter of branches accounted for 9% and 12% of the variance in protein ($F=5.34$, $p=0.017$, $r^2=0.09$) and phosphorus levels ($F=14.21$, $p=0.001$, $r^2=0.12$), respectively, and was negatively associated with both dependent variables. Calcium level increased with age of the trunk ($F=4.71$, $p=0.021$, $r^2=0.15$) while fibre content increased with distance from water ($F=4.62$, $p=0.046$, $r^2=0.20$).

Immersion in water significantly reduced levels of protein, phosphorus, and unspecified material in trunks of alders ($p<0.05$). Fibre content varied directly with age ($F=27.98$, $p=0.007$, $r^2=0.88$).

Birch

Nutrient composition of trunks of birch trees was not associated with any of the independent variables entered into the analyses. The most important factor affecting the nutrient regimen of branches was their diameter. That variable was negatively associated with protein ($F=28.52$, $p=0.000$, $r^2=0.54$), calcium ($F=21.72$, $p=0.000$, $r^2=0.48$), phosphorus ($F=9.36$, $p=0.001$, $r^2=0.12$), and levels of unspecified material ($F=7.29$, $p=0.002$, $r^2=0.36$). It was inversely related to leaching rates ($F=8.35$, $p=0.017$, $r^2=0.43$) while directly related to fibre content ($F=14.36$, $p=0.000$, $r^2=0.36$). Increased distance from water ($F=11.90$, $p=0.000$, $r^2=0.11$) and growth rate ($F=3.31$, $p=0.032$, $r^2=0.05$) also resulted in increased fibre content in the bark of branches. Distance from water negatively affected amounts of unspecified material ($F=8.01$, $p=0.003$, $r^2=0.23$). Phosphorus content, which declined from fall to spring, was the only component significantly affected by overwinter storage in water.

V. DISCUSSION

Beavers residing in northern latitudes are well adapted to winter conditions. Adaptations include isolating themselves from the external environment by restricting winter activity to the lodge and food cache. The lodge and ice form effective barriers to predation during winter. As well, the environment of the lodge provides protection against thermal stress during extreme weather conditions. Stephenson (1969) recorded an average daily temperature fluctuation of 0.8 to 1.6°C within a beaver lodge while average ambient daily temperature ranged from -21.0 to -6.8°C.

Beavers also respond to northern winter conditions through a series of energy-conserving physiological adaptations. These include cessation of skeletal growth and decrease in body weight in subadults during winter as well as decreased metabolic activity as indicated by a reduction in the size of the thyroid gland (Aleksiuk and Cowan 1969). Body fat is deposited during late summer and fall, conserved during winter, and mobilized in spring when ice breaks up and activity increases. Thus, beavers adapt to a low quality diet during winter by severely restricting energy expenditure.

Novakowski (1967) studied the energetics of beaver colonies at Wood Buffalo National Park and concluded that, based on the energy contained in wood and bark in their food caches, three of five colonies examined had a winter energy deficit. Aleksiuk (1970) suggested that because beavers do not consume wood, Novakowski (1967) had greatly overestimated the energy available to the colonies while underestimating effects of the winter metabolic depression. However, since the effects of immersion in water were not examined, Aleksiuk (1970) may have overestimated available energy as well. In his study area, willow was the principal winter food of beavers and my data indicate that, during immersion in water, nutrients are rapidly leached from that genus.

Since nutrient levels in winter foods of beavers are generally low, it is important that the foods selected are adequate for the maintenance of a colony, particularly since the demands of gestation, parturition, and lactation occur in late winter and spring. Thus, a logical strategy would be to select those classes of vegetation highest in energy and nutrition. Nudds (1980) reported that feeding strategy of deer (*Odocoileus* spp.) shifts from specialized in mild weather to generalized in severe weather. If this is the general case for herbivores, beavers, which are not forced to forage under adverse conditions,

should selectively attempt to optimize the nutrient content of vegetation in food caches. In fact, Jenkins (1978) reported that beavers removed small pieces of bark from trees, presumably to assess their nutritional value. Similar sampling by beavers was observed at Elk Island National Park, which, coupled with observed foraging patterns, indicates selective use of woody vegetation by beavers in that area.

A. Patterns of Selection

Jenkins (1975) reported that the species selected by beavers depended on their diameter and that selection was absent when variance in diameter was low. An important aspect of the present study is that it indicates that a number of factors affect food preferences of beavers and that important factors may vary with plant species. Thus, whether beavers prefer or avoid a tree species may depend on characteristics such as diameter, age, or growth rate of that species and those of other plant species in the area. At Elk Island National Park, both age and diameter affected selection of aspen poplar with aspen of small diameter avoided; however there was no apparent relationship between selection and variance of tree diameter.

Many other studies (Aldous 1938, Shadle *et al.* 1943, Hall 1960, Brenner 1962, Northcott 1971, Slough and Sadleir 1977) indicated that aspen poplar has the highest preference rating of any tree species. Most, however, were conducted in areas where balsam poplar was not available or else it was combined with aspen during data analysis. At Elk Island National Park, balsam poplar is generally preferred over other tree species, although the strength of selection depends on characteristics of both balsam and aspen poplar. However, it appears that the criteria for selection of balsam poplar are less stringent than those of other species. There is selection in favor of all classes of balsam poplar and a discriminant function analysis could only weakly discriminate between cut and uncut trees, indicating little difference in the characteristics of the two groups.

For aspen poplar, basal diameter was a major factor governing selection, with beavers tending to cut the largest trees. This differs from most other studies of selection. Pinkowski (1983) found that in North Dakota, aspen poplars cut down by beavers ($\bar{x}$=10.2 cm) were smaller than those left standing ($\bar{x}$=12.0 cm) and that there was a strong tendency for the diameter of cut trees to decrease with increasing distance from

water. Similarly, Hall (1960) reported that the use of small diameter aspen poplar (5.0 cm) exceeded their availability; this pattern was attributed to the suitability of the size class as building material.

For species other than aspen poplar, there was no consistent relationship between diameter and selection. These results are similar to those of Chabreck (1958) who could find no evidence for selection of certain diameters. Most other studies, however, indicate selection for small size classes. In Ohio, Nixon and Ely (1969) found that trees less than 5 cm in diameter were selected most often, while Henry and Bookhout (1970) reported that 90% of the trees cut by beavers were less than 7.5 cm in diameter. In Massachusetts, Jenkins (1980) indicated that selection based on diameter increased and the size of cut trees decreased with increasing distance from water.

At Elk Island National Park, the only obvious size-distance relationship was a tendency for the range of sizes of aspen poplar removed from cutting sites to decrease with distance, which is consistent with the results of Jenkin's (1975) study where the size range of cut trees decreased with distance from water. Since most trees cut down on his study area were less than 6 cm in diameter, it is likely that the majority of those trees were completely removed. These patterns are logical from an energetic standpoint. At some point, energy expended to transport small items long distances across land must exceed benefits obtained from ingesting them. Similarly, moving large, heavy materials short distances to water may be beneficial while the energy required to move identical items over long distances may be excessive. Hence it may be adaptive to concentrate increasingly on items of optimal size as distance from water increases.

Few studies examined the size of materials removed from cutting sites by beaver. However, Shadle (1954) measured cuttings used in construction of a dam. Since most wood in the dam had been peeled, this method likely slightly underestimated the size when cut. However, the average diameter of poplar (*Populus* spp.) removed by beaver as calculated from his data was approximately 8.5 cm, and the largest, 16 cm. This compares to an average diameter of 7 cm for poplar removed from cutting sites at Elk Island National Park. The discrepancy is probably caused by underestimation of removal of items too small to be used as structural material by Shadle's (1954) method.

The structure of food caches observed at Elk Island National Park was similar to that recorded by Slough (1978). He indicated that alder was found at the surface of food caches while aspen and willow were found throughout caches. Slough (1978) attributed the presence of alder on the surface to its low food value and its preferred use as structural material. Structural criteria may also explain size differences between surface and subsurface materials. However, it is more likely that the high buoyancy of large items makes it more difficult for beavers to submerge them. During fall 1982, we presented an adult beaver with balsam poplar logs about 20 cm in diameter. The beaver was unable to dive with them to incorporate them into the food cache although several attempts were made.

The buoyancy of large items largely explains the descrepancy between the size of materials removed from shore and that found in food caches. Large items appear to be transported from shore to the vicinity of food caches where they are stripped of branches and bark. The branches are then incorporated into caches but peeled main stems are often left floating on the surface. The average diameter of freshly peeled wood in caches during 1982 was 6.4 cm compared with 5.1 cm for unpeeled aspen poplar, the second largest food cache material. These large floating branches are frequently blown into open water or shore.

Species composition also differed between shoreline cuttings and food caches, particularly for willow and alder. Seasonal variations in food preferences as suggested by Jenkins (1979) may have contributed to the difference. Between 14 and 21 September, 1983, 21 food caches were examined at Elk Island National Park, 33% (n=7) of which contained willow. Twenty-five food caches, including the previous 21, were examined about three weeks later and the percentage of caches containing willow, had more than doubled, to 72% (n=18). The frequency of occurrence of alder during the same period rose from 14% (n=3) to 24% (n=6); however, in many cases we were unable to find areas where beavers had cut alder, which suggests that they ranged over long distances to obtain it.

Seasonal use of willow by beavers may be related to its high leaching rate. Since nutrients appear to be rapidly depleted by immersion in water, it would be advantageous to minimize the period of winter storage. This could be accomplished by cutting willow in

late fall and ingesting it during early winter. The high density of ungulates may also contribute to this pattern of use for willow. Browsing moose (*Alces alces*) feed on willow principally during winter thus allowing regeneration during the rest of the year. By delaying cutting until late fall, beavers would maximize the time available for willow to recover from the previous winter's browsing by ungulates.

Increased selection for willow and alder in young colonies may result from the use of those shrubs as structural material. Recently established beaver lodges are usually constructed of small-diameter unpeeled wood. By using willow and alder for this purpose, it would be possible for beavers to conserve preferred aspen and balsam poplar for use as food. A concomitant result of removing shrubs would be to accelerate the invasion of shade-intolerant poplars which are a source of high-quality winter food.

B. Factors Affecting Selection

Nutrition

A significant feature of the present study was the close association between preference at the species level and nutrient content. Of the three principal tree species occurring at Elk Island National Park, balsam poplar had the highest preference rating. In three of eight categories, that species appeared to have the most favorable concentrations of assayed materials (Table 10). As well, it placed second in an additional three categories. Aspen poplar, which ranked second in preference, placed first in one category and second in four others. Birch was strongly avoided by beavers and ranked high in only one category analyzed.

The relationship between nutrition and selection by beavers has seldom been studied although numerous studies on nutrient selection by ungulates and lagomorphs have been conducted. Of the ungulates, moose have foraging patterns most comparable to those of beavers. Moose feed largely on aquatic vegetation during summer and shift to a diet of woody vegetation in late fall and winter. Like beavers, hares (*Lepus* spp.) have a caecum and rely heavily on a diet of woody vegetation. Moose and hares, however, browse mainly on the current annual growth of twigs while beavers rely mainly on bark.

In the present study, protein level was not closely associated with selection at the species level. Alder had the highest protein levels but selection for it was neutral. These results differ from those of Lindlof *et al.* (1974) who studied nutrition-preference relations of mountain hares (*Lepus timidus*) and found a strong positive correlation between protein content and selection (r=0.90).

Sinclair *et al.* (1982) indicated that sufficient levels of protein were extremely important to snowshoe hares. They reported that captive hares rapidly lost weight when protein content of their food dropped below 11% and suggested that hares in the wild select forage of greater than average protein concentration to overcome the paucity of protein in most woody vegetation. Levels of protein in the present study were much lower than the threshold reported by Sinclair *et al.* (1982). Alder, which had the highest protein content of all food cache materials, contained only 6.5% protein in fall and 4.9% after overwinter immersion, less than one-half the reported threshold for hares. Balsam poplar, the most common food cache material, had levels of 4.7% in fall and 3.8% by the following spring, only one-third of the threshold. Three factors may ameliorate the effects of the low protein levels observed: (1) the protein requirement of beavers may be inherently lower than that of hares, (2) the winter metabolic depression may greatly reduce protein demand, and (3) as indicated for hares (Sinclair *et al.* 1982), beavers may select only forage of higher than average quality.

However, the greatest demand for protein by beavers likely occurs in spring, coincident with late gestation and lactation. Since alder, which contains high concentrations of protein, is usually placed on the surface of food caches, it generally remains unavailable until the spring thaw. Thus, the pattern of winter storage for alder may make available a reserve of protein for reproductive females in early spring. A second effect of the position of alder in food caches may be a reduction in levels of plant secondary compounds. Bryant (1981a) reported that green alder (*Alnus crispa*) contains high levels of pinosylvan methyl ether, which is highly toxic to hares. Since ethers with low carbon numbers are slightly soluble in water (Morrison and Boyd 1977), the long period of overwinter storage may reduce levels of toxins.

Lindlof *et al.* (1974) reported an extremely high positive correlation between mountain hare forage preference and phosphorus content (r=0.97). Although levels of

phosphorus and preference by beavers appeared to be related, levels among species were not statistically different. In addition, they were only about one-half of the phosphorus levels of 0.12 to 0.20% recorded by Lindlof *et al.* (1974).

There is, however, evidence that in mammals, phosphorus uptake is controlled by calcium uptake. Clark (1969) conducted experiments on laboratory rats (*Rattus norvegicus*) and found that the proportion of phosphorus absorbed did not vary according to the requirements of the animals but was closely associated with the proportion of calcium taken up. Barkley *et al.* (1980) constructed a model to simulate the diet of brown lemmings (*Lemmus sibiricus*) and postulated that excessive levels of calcium would cause nutrient depletion because of resultant poor absorption of phosphorus.

Calcium levels in beaver forage were greater than the 0.34 to 0.91% reported for mountain hare browse in winter by Lindlof *et al.* (1974) but similar to levels recorded in summer by Lindlof *et al.* (1978). At the plant species level, selection of forage by beavers is associated with calcium level, a pattern similar to that of mountain hares (Lindlof *et al.* 1978). This suggests that calcium levels in woody vegetation are insufficient to restrict phosphorus uptake. Because of the low levels of phosphorus available to beavers, it appears that an appropriate strategy would be to select species with levels of calcium which, although high, do not exceed a beaver's ability to absorb it, thereby maximizing phosphorus uptake.

Plant fibre consists largely of cellulose which is among the most indigestible fractions of plant material (Radwan and Crouch 1974). Several studies have been conducted with ungulates, which are highly adapted to cellulose digestion through the process of ruminal microbial fermentation. For both moose (Oldemeyer *et al.* 1977) and mule deer (*Odocoileus hemionus*)(Short 1966), digestibility was determined by fibre content. Additional studies by Radwan and Crouch (1974) indicated that the order in which vegetation was selected by black-tailed deer (*O.h. columbianus*) was determined by cellulose digestibility. Selection against high cellulose levels by beavers may be more pronounced. Beavers are capable of digesting about 30% of the cellulose in their diet (Currier *et al.* 1960, Hoover and Clark 1972). This is comparable to lagomorphs but considerably lower than the range of 41 to 82% reported for ruminants (Currier *et al.* 1960). At Elk Island National Park, selection of tree species is strongest for poplars

which are characterized by low fibre content.

Hazel was not sampled during shoreline vegetation surveys or nutrient analysis in 1982. However, because it was a common constituent of food caches, in fall 1983, the selection of shrubs was examined by establishing a 25 m transect with 4 m^2 vegetation plots at 5, 15, and 25 m directly behind 26 beaver lodges. Since snowshoe hare browse in upland sites is uncommon (personal observation), all browsing not identified as ungulate was assumed to have been by beavers. Only 5% (n=211) of the shrubs and 6% (n=51) of the hazel had been browsed. This compares with 42% (n=2265) of the trees larger than 2 cm in diameter in all areas sampled in 1982 and indicates that there is relatively little use of shrubs by beavers.

Nutritionally, hazel appears to be low quality forage. Peek *et al*. (1976) indicated that crude protein levels in hazel were much lower than those in aspen poplar or willow. Similarly, phosphorus levels were lower in hazel than in the other two species, although calcium content was much greater. Other studies have indicated that cellulose content of hazel was comparable with that of alder (Radwan and Crouch 1974). If these relationships are similar to those at Elk Island National Park, hazel ranks high in calcium content but low in most other nutrients. Further, low foraging rates on hazel and its relative unimportance as a source of bark suggest that hazel is of little significance to beavers as forage.

Other Factors

While selection among species of woody vegetation appears to be closely associated with overall nutrient levels, the relationship between nutrient concentrations and intraspecific selection is not as evident. However, several factors other than macronutrient levels may influence selection within a species. Some of the obvious factors are:

1. Levels of micronutrients that were not considered in the present study.
2. Levels of toxic plant secondary compounds.
3. The degree to which benefit obtained from a food exceeds the energetic cost and risk associated with foraging for it.

In the last case, energy cost and the risk of predation would increase with distance from water and time required to obtain forage. Ultimately, however, selection is probably determined by a number of interacting factors.

Peek *et al.* (1976) indicated that nutrient levels of plant species browsed by moose were higher in wet and mesic sites than in dry upland areas. At Elk Island National Park, most areas are wet to mesic. However, distance from water was the principal influence on nutrient concentrations in aspen poplar and significantly affected those of balsam poplar. The pronounced influence on aspen poplar likely reflects its association with mesic upland sites as compared to balsam which is common on moist shorelines. Although it appears that beavers can obtain considerable nutritive benfit from using aspen growing long distances from water, the proportion of aspen cut was greatest within 8 m of water (Fig. 5), which suggests that, where aspen poplar is concerned, the benefits of restricting foraging distance exceed those of maximizing nutrient content.

Restricted foraging distance was most evident for birch. Although, for this species, distance from water is directly related to fibre content, the strong avoidance of birch growing more than 17 m from water probably also reflects the limited benefits obtained from ingesting it.

Nutrient levels in aspen poplar increased as diameter decreased, which is comparable to the results of Hjeljord *et al.* (1982) who reported that the digestibility of moose forage was inversely related to its diameter. Despite this relationship, beavers selected against high quality aspen poplar trees by selectively cutting the largest individuals available.

In fall 1983, I briefly examined the distribution of branches on poplars by constructing a 95% confidence interval around the mean diameter found in food caches for each tree species and counting the number of branches within this range available on trees of various diameters. The number of branches within the confidence interval on balsam poplars varied linearly with basal diameter whereas with aspen poplar the pattern was more complex (Fig. 10). Here, the number of suitable branches increased to 15 on trees 14 cm in diameter, thereafter declining to 8 at 18 cm. The number then increased exponentially as tree diameter increased. It therefore appears that beaver can maximize the amount of woody material obtained from aspen by cutting trees about 14 cm in diameter or very large trees. This, however, fails to explain why small trees are not taken since there are almost as many suitable branches on an aspen poplar 14 cm in diameter as on a 25 cm tree and the effort to cut down trees increases in relation to the square of the

diameter.

A possible explanation involves the role of plant secondary compounds and competing herbivores. The density of moose at Elk Island National Park is exceptionally high. Telfer and Cairns (1978) reported that 436 moose inhabited the area (2.25 moose per km^2). This compares with densities of 0.64 per km^2 in similar habitats near Rochester, Alberta (Mytton and Keith 1981) and 0.10 per km^2 in marginal habitat in northeastern Alberta (Skinner and Westworth unpubl data). Browsing pressure by native ungulates on aspen poplar is generally much greater than that on balsam poplar (personal observation, Westworth pers comm). Bryant (1981b) reported that aspen poplar responded to heavy browsing by snowshoe hares by producing adventitious shoots which contained significantly greater concentrations of secondary compounds than mature-form plants. Further, laboratory experiments by Baldwin and Schultz (1983) indicated that poplars (*Populus x euroamericana*) responded to damage inflicted on nearby plants by elevating their production of phenolics by as much as 58%. Thus browse on a single aspen ramet may cause increased levels of phenols in a number of others. Bryant and Kuropat (1980) presented data which indicated that browse preferences for moose and hares were significantly and negatively correlated with concentrations of plant secondary compounds. They also reported that levels of those compounds decline as tree diameter increases. While hares and moose probably have little impact on trees 14 cm in diameter, they may, by browsing, raise levels of secondary compounds in small size classes to greater concentrations than are found in large trees. Since the ability of rodents to detoxify secondary compounds increases with increasing stomach complexity (Freeland and Janzen 1974) and beavers have a simple stomach, their ability to deal with toxic compounds is probably low. The result may be an avoidance of small size classes of aspen poplar.

Beavers also selected in favor of young aspen poplar in any diameter class. Other studies have indicated that young vegetation is characterized by higher nutrient levels, lower amounts of fibre, and greater digestibility by ungulates than older material (Hjeljord *et al.* 1982, Vangilder *et al.* 1982). At Elk Island National Park, the age of aspen poplar trees has little effect on nutrient concentrations. However, since beavers select aspen that are large as well as young, they are, in effect, selecting trees with a high annual rate of growth. Chabreck (1958) found that beavers selected fast-growing loblolly pine

(*Pinus taeda*). Because crown size was directly proportional to growth rate, he suggested that beavers were selecting rapidly growing trees to increase the amount of forage obtained from each tree.

Nutrient concentrations in balsam poplar depended primarily on the age of the tree whereas trees selected most often were those with a high rate of growth. However, it would be unfeasible for beavers to select trees solely on the basis of age since the youngest and most nutrient-rich trees are also the smallest available. It would therefore be possible for beavers to expend more energy to find and remove those items than could be obtained from eating them. If the relationship between growth rate and crown cover (Chabreck 1958) applies to balsam poplar, beavers may be attempting to maximize the forage available from any given age of tree by selecting the fastest-growing individuals, perhaps by sampling bark on standing trees (Jenkins 1978). As well, nutrient content would be increased by selecting the younger and therefore faster-growing trees of any diameter.

Variability in Diet

Although beavers at Elk Island National Park appear to select species high in overall nutrition, even plant species low in nutrients were common in food caches. For example, birch, which was low in most nutrients analyzed, comprised 11% of the material in food caches. Westoby (1978) suggested that there are several situations in which a varied diet is beneficial: (1) A variety of foods is likely to be taken where considerable effort is required to search for preferred forage. (2) Optimal foods may vary depending on search costs and nutrition. (3) If the optimal diet is variable, sampling behavior may be used to assess forage quality. (4) Complex diets provide a greater range of nutrients than simple diets. For example, at Elk Island National Park, protein intake is maximized by feeding on alder while poplars provide the greatest concentrations of most other nutrients.

Plant secondary compounds may also produce varied diets (Freeland and Janzen 1974). Since plant toxins from different species may have antagonistic or synergistic effects, Freeland and Janzen (1974) suggested that variable diets can act as a mechanism for simultaneously maximizing the intake of food and detoxifying harmful plant compounds.

C. Population Trends

Density of Colonies

The reported accuracy of aerial surveys for censusing beaver varies widely. Slough and Sadleir (1977) observed 8 colonies from the air and 48 on the ground, an accuracy of 17%. In mainly coniferous habitats in Newfoundland, 61% of the beaver colonies were observed from fixed-wing aircraft while 81% were located from helicopters (Payne 1981). Swenson *et al*. (1983) reported observation efficiencies of 70 to 100% from fixed-wing aircraft in Montana. It therefore appears that in 1982, the accuracy of the beaver survey of Elk Island National Park (83%) was about average, despite poor survey conditions.

The density of colonies at Elk Island National Park (0.94 colonies per km^2) appears to be one of the highest reported in Canada. Densities in good quality habitat in Newfoundland ranged from 0.18 to 0.26 colonies per km^2 (Bergerud and Miller 1977). In Saskatchewan, Gunson (1970) reported colony densities of 0.11 to 0.34 per km^2 in low quality habitats and 0.44 per km^2 in high quality habitat. Larson and Gunson (1983) examined 20 areas across Canada and reported that colony densities at Elk Island National Park between 1973 and 1976 averaged 0.93 per km^2; this density was exceeded only by the number of colonies at Riding Mountain National Park (1.06 per km^2). They further suggested that 1.2 colonies per km^2 is the maximum potential density for Canada. Because of high beaver density in the study area, most suitable areas have, at some time, been occupied by beavers (Fig. 1). During foraging surveys, we visited over 60 bodies of water, only two of which showed no sign of occupancy.

Parks Canada censused beaver colonies from 1963 to 1981. Ground surveys were conducted in 1963, 1968, and 1970 and there were annual aerial surveys from 1973 to 1976. A survey was also flown in early spring 1981; however, because the results are inconsistent with those of earlier surveys and that conducted during the present study, it is not considered here. The survey data indicate that the number of colonies increased slowly from 1963 to 1968 and then increased rapidly until 1976. Between 1976 and 1982, the number of active colonies appears to have declined slightly

(Fig. 11).

Beaver colonies in the park are frequently abandoned and later recolonized. Survey data indicate that 92% (n=65) of 71 colonies observed in 1963 had been abandoned at least once by 1982. However, as of 1982, 43% (n=28) of the 1963 colony sites were occupied. Because regeneration of aspen and balsam poplar is relatively slow, this may indicate that beavers recolonizing previously abandoned areas are occupying relatively low quality habitats.

Besides affecting population densities (Gunson 1970, Boyce 1981b), habitat quality has an influence on other demographic characteristics. Huey (1956) found that litter size in colonies using willow as food averaged 2.1, compared with 4.2 for colonies in aspen-dominated areas. In Saskatchewan, yearling beavers lost weight over winter where poplar constituted only 9% of food cache materials while weight gains were recorded when caches contained 45% poplar (Pearson 1960). In Colorado, beaver populations increased more rapidly and had a greater number of beavers per colony in aspen-dominated areas than in locations dominated by willow (Yeager and Rutherford 1957). Therefore, to determine the relationship between habitat, food, and population trends, a knowledge of colony size and reproductive rates is fundamental.

Colony Size

Although there are rare reports of beavers moving between colonies (Beer 1955, Busher *et al*. 1983), family groups of beavers generally occupy exclusive home ranges (Brenner 1967, Aleksiuk 1968, Bergerud and Miller 1977, Boyce 1981a). Family groups usually comprise an adult male and female, kits, yearlings and sometimes 2-year-old offspring (Novakowski 1965, Bergerud and Miller 1977, Svendsen 1980b). Since beavers are often sexually mature before they are 2 years old (Larson 1967), potentially reproductive individuals frequently remain with their parents. This is most likely to occur in areas where the saturation of high quality habitat with colonies causes high mortality among dispersing beavers (Bergerud and Miller 1977, Boyce 1981a). The result is many individuals per colony in saturated habitats of high quality.

Schwanke and Baker (1977) reported 8.6 beavers per colony at Elk Island National Park. This compares with an average colony size of 6.0 in Ohio (Svendsen 1980b).

Bergerud and Miller (1977) found that colonies in various regions of Newfoundland averaged from 2.2 to 5.1 individuals while Payne (1982) reported an average of 3.5 in that province. Novak (1977) calculated a mean colony size of 7.6 beavers near North Bay, Ontario. In Nevada, areas of high and low colony density were studied over two years (Busher *et al.* 1983). The area with high colony density had more than 9 individuals per colony even though kits were not counted. Moreover, 2-year-olds were present in 7 of 8 observations of colonies. This compares with an average of 5 beavers per colony (including kits) in an area of lower colony density. In that area, 2-year-olds were present in only 2 of 8 observations. The colony size for Elk Island National Park reported by Schwanke and Baker (1977) therefore appears typical of good quality saturated habitat.

Reproduction

Gunson (1970) suggested that reproduction by beavers is density dependent. Thus, reproductive females are likely to produce low numbers of embryos and kits in areas saturated with colonies.

Several North American workers have reported litter sizes of approximately 2.7 young per reproductive female (Bergerud and Miller 1977, Svendsen 1980b, Wigley *et al.* 1983). In southern Russia, reproductive Canadian beavers have an average litter of 3.2 young (Danilov and Kan'shiev 1983). Brenner (1964) reported 5.5 young per female in Pennsylvania while in Saskatchewan, there were 4.1 young per reproductive female (Gunson 1970).

Pearson (1960) indicated that the average litter size of 3.5 in a stable population of beavers at Prince Albert National Park, Saskatchewan was exceeded by the average of 6.3 young per reproductive female in a rapidly expanding population at Elk Island National Park in 1958. By 1975, litter size in the latter area had decreased to an average of 5.1, an indication that the population was entering a period of stability (Schwanke and Baker 1977). In 1982, based on embryo and placental scar counts, 4 reproductive female beavers produced an average of 2.8 (range 2 to 5) offspring per litter. While this appears to be about average for North America, it is much lower than litter sizes reported by Pearson (1960) and Schwanke and Baker (1977) for the same area. Although the data are insufficient to be conclusive, they indicate that reproductive rates may be decreasing

because of a decline in habitat quality.

Habitat

The distance that beavers will travel inland to obtain food may provide an indication of habitat quality. In areas with an abundance of preferred foods, foraging likely occurs primarily near water. In Ohio, Brenner (1967) reported beavers foraging as far as 750 m from shore while Henry and Bookhout (1969) recorded maximum distances of 50 to 75 m. Yeager and Rutherford (1957) found maximum foraging distances of 90 m in Colorado.

At Elk Island National Park, mean maximum foraging distance was 20 m, while the maximum observed during the foraging inventory was 78 m, recorded in a willow flat. The cuttings farthest from open water were observed at a pond surrounded by conifers. At that location, the conifers adjacent to the pond were unused while aspen poplar growing approximately 200 m from open water had been used extensively. In both areas, beavers had constructed a complex network of canals to facilitate removal of material. These observations compare with those of Schwanke and Baker (1977). They reported a mean maximum foraging distance of 22.7 m and a maximum of 41 m at 10 colonies they examined at Elk Island National Park between 1974 and 1976.

The distance inland that beavers foraged at Elk Island National Park was related primarily to the total amount of timber available within 30 m of water rather than the availability of particular species. The inability of the analysis to define important species likely results from the absence of selection for plant species within 10 m of water. As the total amount of timber in an area increases, the distance travelled to obtain forage decreases and most cutting will be less than 10 m from water. The availability of birch also negatively affected foraging distance. Since birch is avoided by beavers, there would be little incentive to range over long distances in birch-dominated forest, particularly since selection against birch is greatest where distance from water is high. Moreover, in many areas, birch tended towards dense monospecific stands. Hence, a reduction in the amount of birch may imply the greater availability of preferred species.

At Elk Island National Park, no differences in habitat or forage availability between active and abandoned colony sites or among colony age classes were detected. In Alaska,

Boyce (1981b) reported that colony sites occupied for a single winter were characterized by a lower biomass of potential food cache material than sites occupied for two or more consecutive years. One-year-old colonies could not be positively identified in the present study but I was able to examine the characteristics of active and abandoned colonies less than 3 years old. However, there was no apparent relationship between any habitat variable, including total basal area, a variable similar to biomass, and status of the colony. The results were similar when habitat was compared among colonies of different ages. These results are comparable to those of Henry and Bookhout (1970) who were unable to detect differences in vegetation in the proximity of colonies less than 3 years old and those older than 5 years.

Although habitats within 30 m of water did not differ significantly among colonies ($p>0.05$), there were slight although insignificant ($p>0.05$) differences in the quantity of preferred classes of woody vegetation within 10 and within 20 m of water. Within 20 m of shore, age class 4 colonies had a greater density of balsam poplar and young, large aspen poplar (2.47 trees per 100 m^2) than other age classes, which had a range of 1.63 to 2.03 per 100 m^2. Within 10 m of shore, the density of preferred tree classes was only 0.41 per 100 m^2 at age class 1 colonies. This is lower than the range of 0.60 to 0.77 found at other colonies. The oldest surviving colonies in Elk Island National Park appear to occupy areas that have an abundance of winter food, which suggests that those colonies were originally established in areas particularly rich in preferred classes of woody vegetation. Lower densities of preferred classes of woody vegetation adjacent to young colonies imply that recent colonization is occurring in relatively low quality habitats.

Schwanke and Baker (1977) used an estimate of foraging distance to assess the area available to foraging beavers at 10 colonies in Elk Island National Park. Areas where foraging had previously occurred were also measured. They calculated that 2.8 ha was the average foraging area available and that a mean of 0.4 ha had already been used. The average age of the colonies studied, based on aerial survey data provided by Parks Canada, was about 3 years. This indicates that, if the entire area available to beavers is of similar quality to that previously used, most areas are capable of supporting a beaver colony for about 20 years. If beavers initially browse in the best areas, the potential life of the colony will be somewhat lower; however, in some ponds beavers are able to

expand the area available for foraging by raising water levels by constructing dams.

The annual rate of growth for aspen poplar at Elk Island National Park (0.43 cm per year) is greater than that reported by Yeager and Rutherford (1957) at high elevations in Colorado (0.16 cm per year) but lower than the 0.70 cm per year observed in New York (Stegeman 1954). Growth rates for balsam poplar (0.44 cm per year) at Elk Island National Park were similar to those of aspen. Since the average diameter of aspen and balsam poplar felled by beavers was 21.4 cm and 17.0 cm respectively, the regeneration of balsam poplar of appropriate size would take over 35 years while that of aspen poplar would approach 50 years. Although these calculations are imprecise, they are an indication that regeneration rates of preferred classes of trees are inadequate for long-term support of the current population of beavers. If decreasing availability of balsam and aspen poplar forces beavers to forage on poor quality vegetation, further reductions in numbers may result from reduced rates of reproduction.

Table 1. Age classification of beaver colonies at Elk Island National Park during 1982 and 1983.

Age Class	Actual Age (Yr)	No. of Colonies	% of Colonies
1	1 - 3	6	22.2
2	4 - 6	9	33.3
3	7 - 9	7	25.9
4	>9	5	18.5
		27*	99.9

*Three colonies were not included in the data analysis because of changes in methods.

Table 2. Relationship of average and maximum foraging distance with major habitat variables.

Variable	F	Prob.	Slope	r^2
Average Foraging Distance				
Total basal area	55.577	0.0000	-0.999	0.589
Basal area of birch	10.433	0.0037	-4.571	0.144
Stem density of shrubs	7.437	0.0120	50.383	0.065
TOTAL				0.798
Maximum Foraging Distance				
Total basal area	15.241	0.0007	-0.832	0.412
Basal area of birch	7.790	0.0101	-6.327	0.144
TOTAL				0.556

Table 3. Use of principal tree species at beaver colonies of various ages at Elk Island National Park.

Distance from water(m)	Aspen poplar				Balsam poplar				Birch			
	No.(%) cut	G	Prob.	Forage ratio	No.(%) cut	G	Prob.	Forage ratio	No.(%) cut	G	Prob.	Forage ratio
Age class 1 (1 to 3 yr)												
11 to 20	24(26)	0.703	0.45		26(46)	17.606	0.00	+0.94	5(4)	44.385	0.00	-2.09
21 to 30	14(11)	0.108	0.82		20(33)	25.216	0.00	+1.53	5(4)	15.180	0.00	-1.49
>30*	1(17)	1.583	0.30		3(33)	1.583	0.30		0(0)	1.583	0.30	
Age class 2 (4 to 6 yr)												
11 to 20	16(24)	5.685	0.02	+0.71	25(25)	11.337	0.00	+0.92	3(2)	30.384	0.00	-2.26
21 to 30	8(6)	1.342	0.34		25(18)	22.857	0.00	+1.50	2(1)	19.785	0.00	-2.24
>30	5(25)	15.638	0.00	-1.17	25(89)	25.169	0.00	+1.41	0(0)	-	-	
Age class 3 (7 to 9 yr)												
11 to 20*	5(12)	4.367	0.13		16(30)	4.367	0.13		11(22)	4.367	0.13	
21 to 30	4(6)	0.515	0.50		6(9)	3.262	0.07		2(2)	5.252	0.02	-1.54
>30*	0(0)	1.122	0.38		2(67)	1.122	0.38		6(40)	1.122	0.38	
Age class 4 (>9 yr)												
11 to 20	1(3)	13.471	0.00	-2.30	29(30)	4.158	0.04	+0.46	31(23)	0.059	0.86	
21 to 30	4(6)	2.015	0.22		8(8)	9.336	0.00	+1.60	3(1)	13.083	0.00	-2.00
>30*	14(56)	2.742	0.37		10(36)	2.742	0.37		1(20)	2.742	0.37	

*Insignificant G-test for goodness of fit. Species are not tested independently.

Table 4. Relationship of age and diameter for uncut aspen poplar and aspen poplar cut down by beavers. Equations are partitioned from a single multiple regression (see text).

Independent Variable	Slope	F	Prob.	Equations
Age Class 1				
diameter	2.064	1207.22	0.000	Y(uncut) = 5.63 + 2.06dia
cut x dia	-0.210	9.43	0.002	Y(cut) = 5.63 + 1.85dia
Age Class 2				
diameter	2.309	1283.14	0.000	Y(uncut) = 9.12 + 2.31dia - 0.18dis
cut x dia	-0.247	10.21	0.002	Y(cut) = 9.12 + 2.06dia - 0.18dis
distance	-0.178	5.21	0.023	
Age Class 3				
diameter	2.286	78.59	0.000	Y = 4.75 + 2.29dia
Age Class 4				
diameter	2.452	592.05	0.000	Y(uncut) = -2.09 + 2.45dia + 0.30dis
cut x dia	-0.476	12.79	0.001	Y(cut) = -2.09 + 1.98dia + 0.30dis
distance	0.301	11.01	0.001	

Table 5. Relationship of age and diameter for uncut balsam poplar and balsam poplar cut down by beavers. Equations are partitioned from a single multiple regression (see text).

Independent Variable	Slope	F	Prob.	Equations
Age Class 1				
diameter	1.770	681.74	0.000	Y = 8.28 + 1.77dia
Age Class 2				
diameter	2.046	2051.18	0.000	Y(uncut) = 4.95 + 2.05dia
cut	-3.439	14.25	0.000	Y(cut) = 1.51 + 2.05dia
Age Class 3				
diameter	1.951	782.38	0.000	Y = 2.07 + 1.95dia + 0.24dis
distance	0.236	9.728	0.002	
Age Class 4				
diameter	2.252	871.90	0.000	Y(uncut) = 5.39 + 2.25dia
cut x dia	-0.234	7.68	0.006	Y(cut) = 5.39 + 2.02dia

Table 6. Relationship of age and diameter for uncut birch and birch cut down by beavers. Equations are partitioned from a single multiple regression (see text).

Independent Variable	Slope	F	Prob.	Equations
Age Class 1				
diameter	1.928	568.11	0.000	Y(uncut) = 6.99 + 1.93dia
cut x dia	-0.945	48.96	0.000	Y(cut) = 11.65 + 0.98dia
cut	4.668	13.91	0.000	
Age Class 2				
diameter	1.792	382.65	0.000	Y = 8.92 + 1.79dia
Age Class 3				
diameter	1.669	456.28	0.000	Y = 9.93 + 1.67dia
Age Class 4				
diameter	1.376	391.95	0.000	Y(uncut) = 13.66 + 1.38dia - 0.09dis
distance	-0.093	11.01	0.001	Y(cut) = 8.16 + 2.03dia - 0.09dis
cut	-5.498	9.57	0.002	
cut x dia	0.654	4.94	0.027	

Table 7. Results of discriminant function analysis: characteristics of trees cut down by beavers and uncut trees.

Species	Variable	Standardized discriminant function coefficient	F	Prob.	Prediction accuracy(%)
Aspen poplar	diameter	1.961	64.27	0.000	
	age	-1.112	38.16	0.000	70.56
Balsam poplar	growth rate	1.000	19.55	0.000	58.95
Birch	growth rate	-0.316	69.83	0.000	
	dist from water	0.937	125.84	0.000	74.14

Table 8. Composition and size of woody material removed from the shore and observed in beaver food caches.

	Removed from Shore			Observed in Caches		
Species	No.	%	Dia(x±s.e.)	No.	%	Dia(x±s.e.)
Aspen poplar	383	37.3	6.5±0.24	60	14.8	5.1±0.45
Balsam poplar	500	48.6	7.4±0.21	125	30.8	3.4±0.20
Willow	14	1.4	3.6±0.38	69	17.0	2.7±0.19
Birch	102	9.9	5.9±0.28	43	10.6	3.9±0.40
Alder	16	1.6	5.8±0.73	39	9.6	3.2±0.42
Hazel	-	-	-	41	10.1	1.4±0.08
Others	13	1.3	-	29	7.1	

Table 9. Contents of the stomachs of 20 beavers collected at Elk Island National Park, 30 April to 10 August, 1982.

Specimen No.	Volume(cc)	% wood	% bark	% other
1	1010	6.3	37.6	56.3
2	350	12.5	12.5	75.0
3	300	5.9	5.9	88.2
4	700	6.3	6.3	87.5
5	200	6.7	6.7	86.7
6	750	13.3	13.3	73.3
7	350	6.3	6.3	87.5
8	625	13.3	53.3	33.4
9	525	5.9	5.9	88.2
10	500	5.9	5.9	88.2
11	350	6.7	66.6	26.7
12	525	13.3	46.7	39.9
13	350	6.7	33.4	60.1
14	600	12.5	81.2	6.3
15	475	20.0	20.0	60.1
16	150	6.7	6.7	86.7
17	400	0	0	100.0
18	200	0	0	100.0
19	425	0	13.3	86.7
20	800	6.7	6.7	86.7
MEAN	479.3	6.3	17.1	74.4

Table 10. Rank of nutrients, fibre, and leaching among plant species before and after winter immersion in water. High ranks are assigned those high in protein, calcium, and phosphorus, and low in fibre and leached material. Ranks <3 are indicated with an asterisk.

	Protein		Calcium		Phosphorus				
Species	Nov	May	Nov	May	Nov	May	Fibre	Leached	MEAN
Aspen poplar	4	2*	2*	2*	5	2*	1*	5	2.9*
Balsam poplar	5	3	1*	1*	1.5*	1*	2*	2*	2.1*
Beaked willow	2.5*	5	4	4	1.5*	3	4	4	3.5
Diamond willow	2.5*	6	5	5	3	6	3	6	4.6
Alder	1*	1*	3	3	4	4.5	5	3	3.1
Birch	6	4	6	6	6	4.5	6	1*	4.9

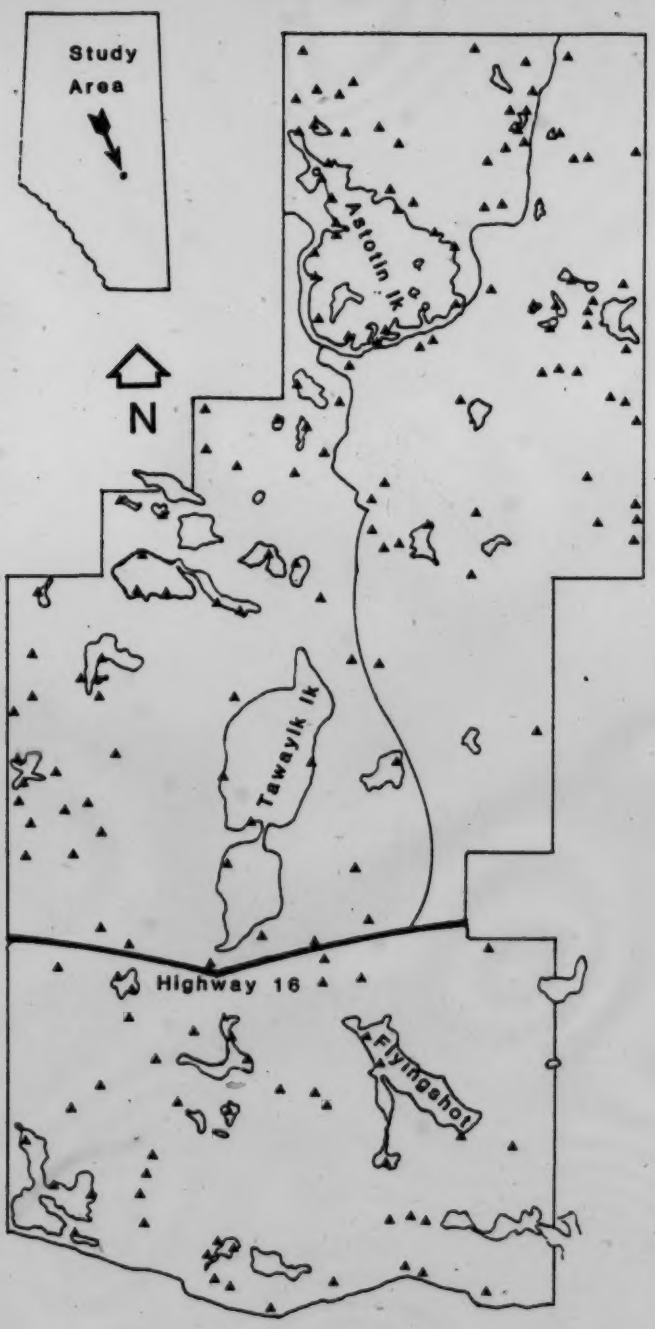

Fig. 1. Distribution of beaver colonies at Elk Island National Park, November 1982.

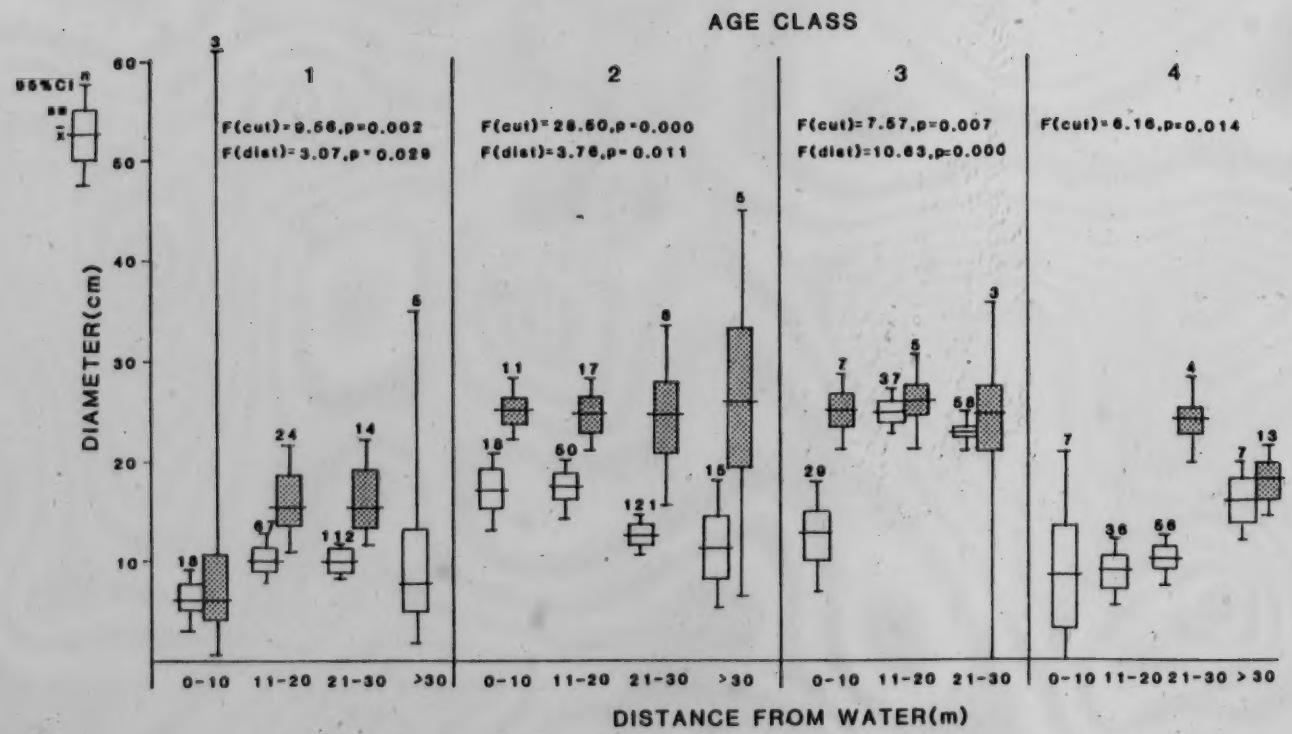

Fig. 2. Distribution of cut and uncut aspen poplar at various distance intervals from water. Open bars and shaded bars represent cut and uncut trees, respectively.

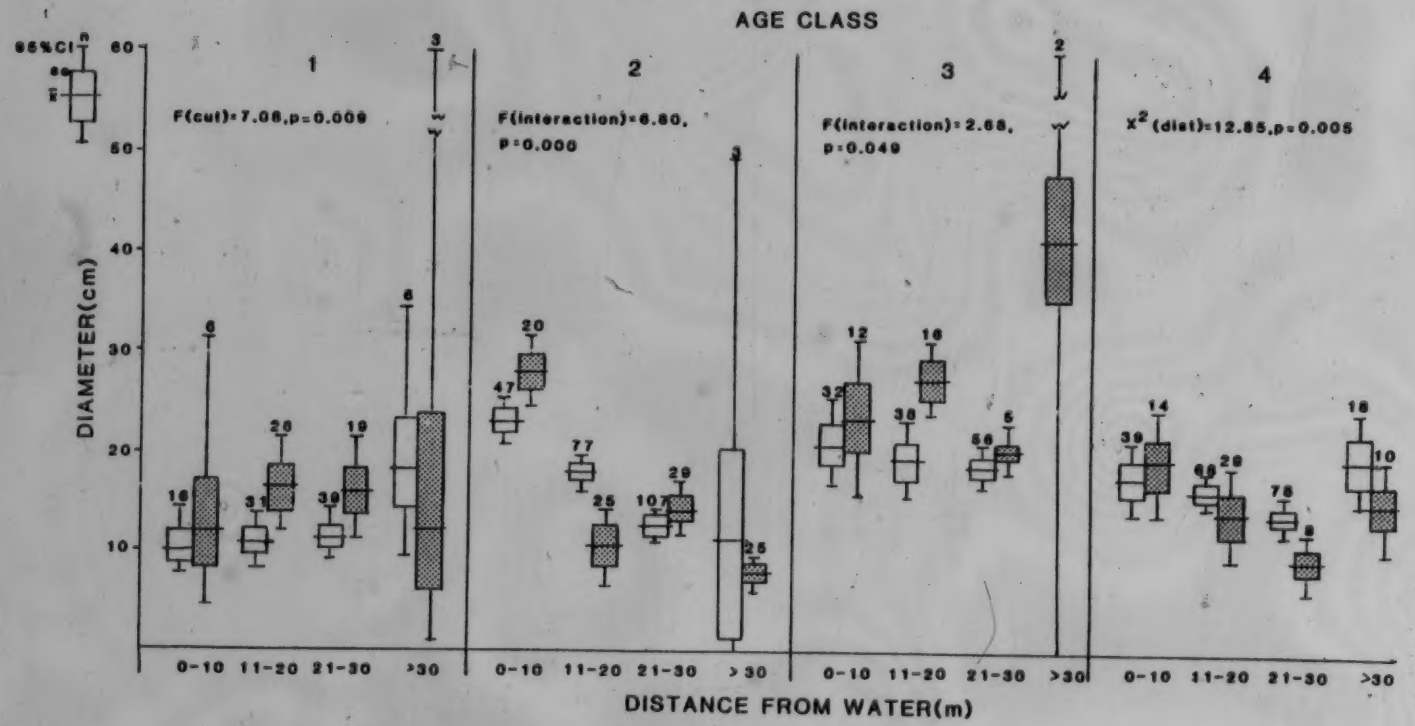

Fig. 3. Distribution of cut and uncut balsam poplar at various distance intervals from water. Open bars and shaded bars represent cut and uncut trees, respectively.

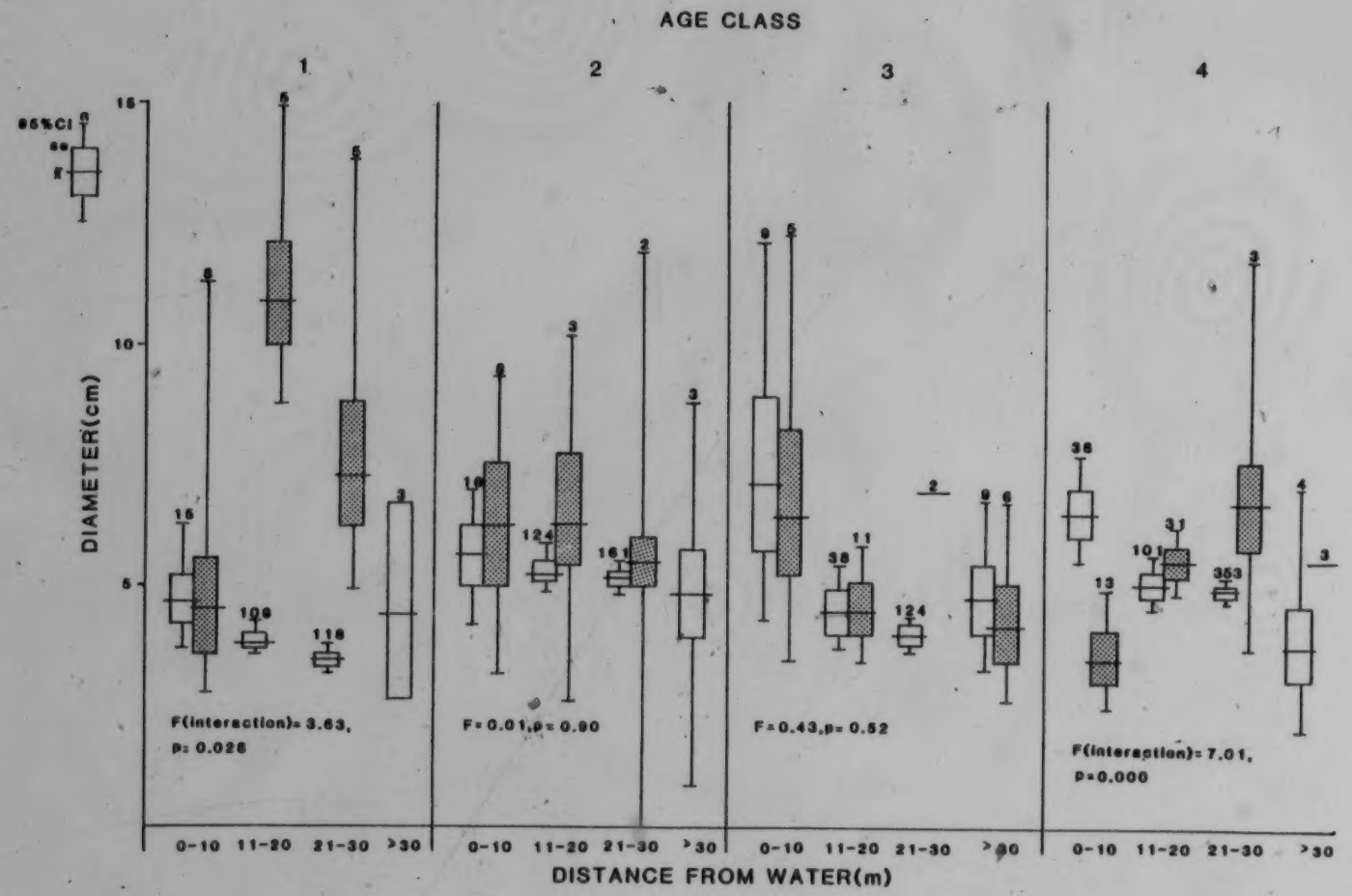

Fig. 4. Distribution of cut and uncut birch at various distance intervals from water. Open bars and shaded bars represent cut and uncut trees, respectively.

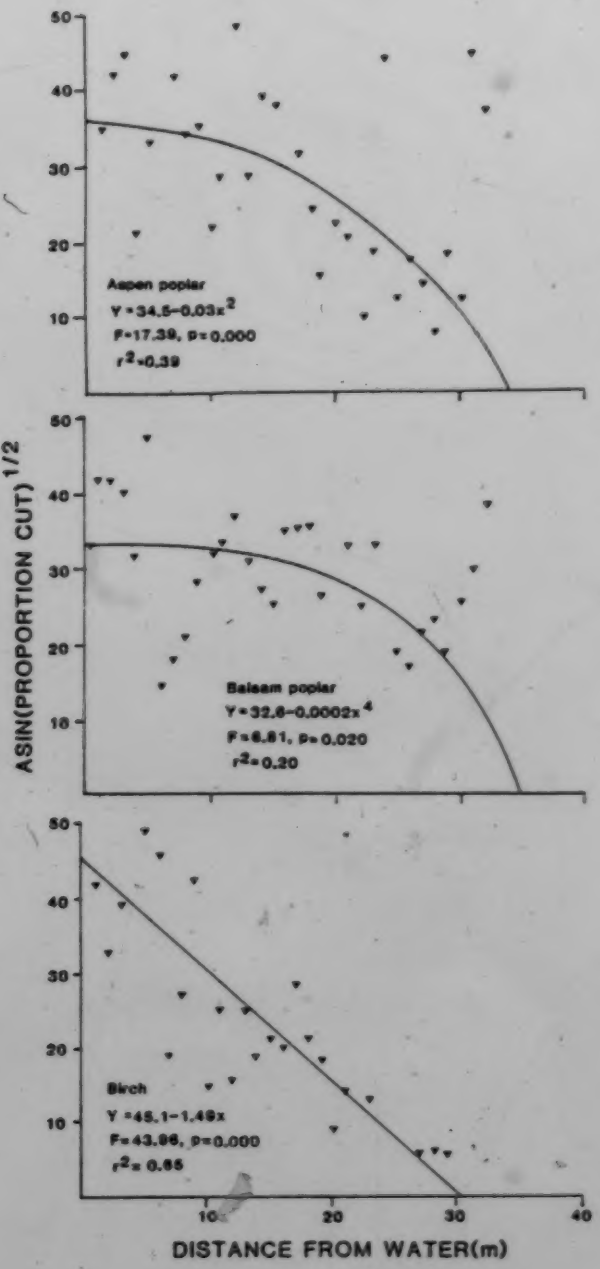

Fig. 5. Proportion of trees cut down by beavers at various distances from shore.

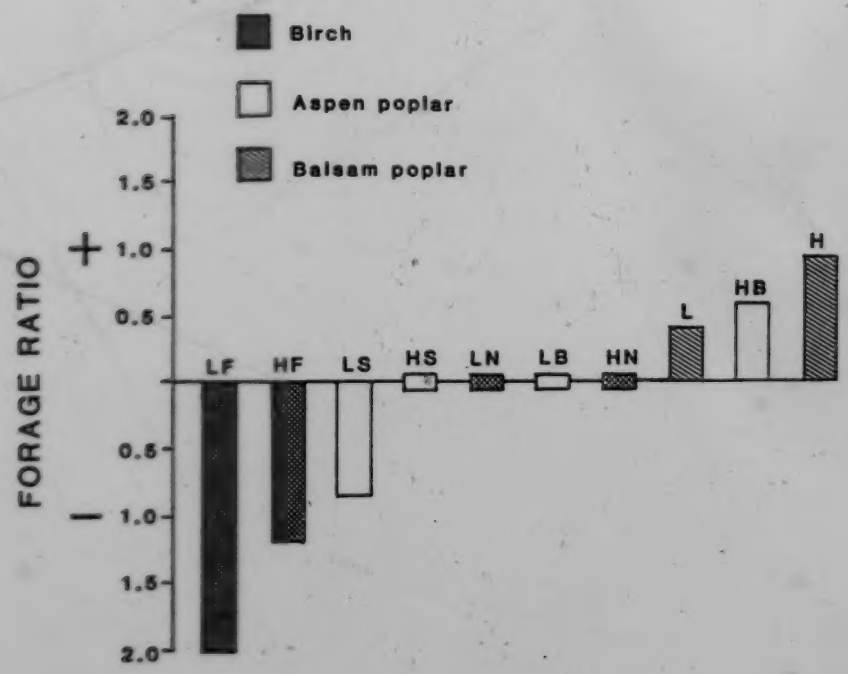

Fig. 6. Preference rating of various classes of woody vegetation based on Jacobs (1974). Growth rate: H-high, L-low; Diameter: B-large, S-small; Distance from water: F-far, N-near.

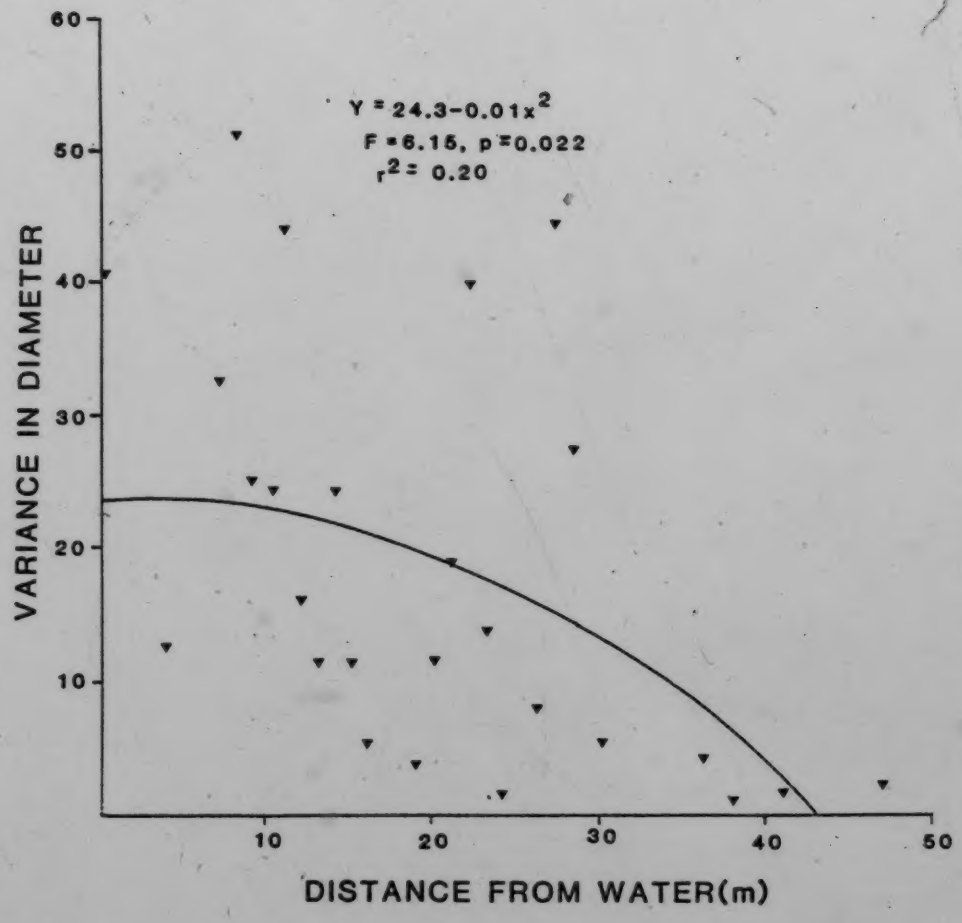

Fig. 7. Relationship of variance in the diameter of aspen poplar removed from cutting sites and distance from water.

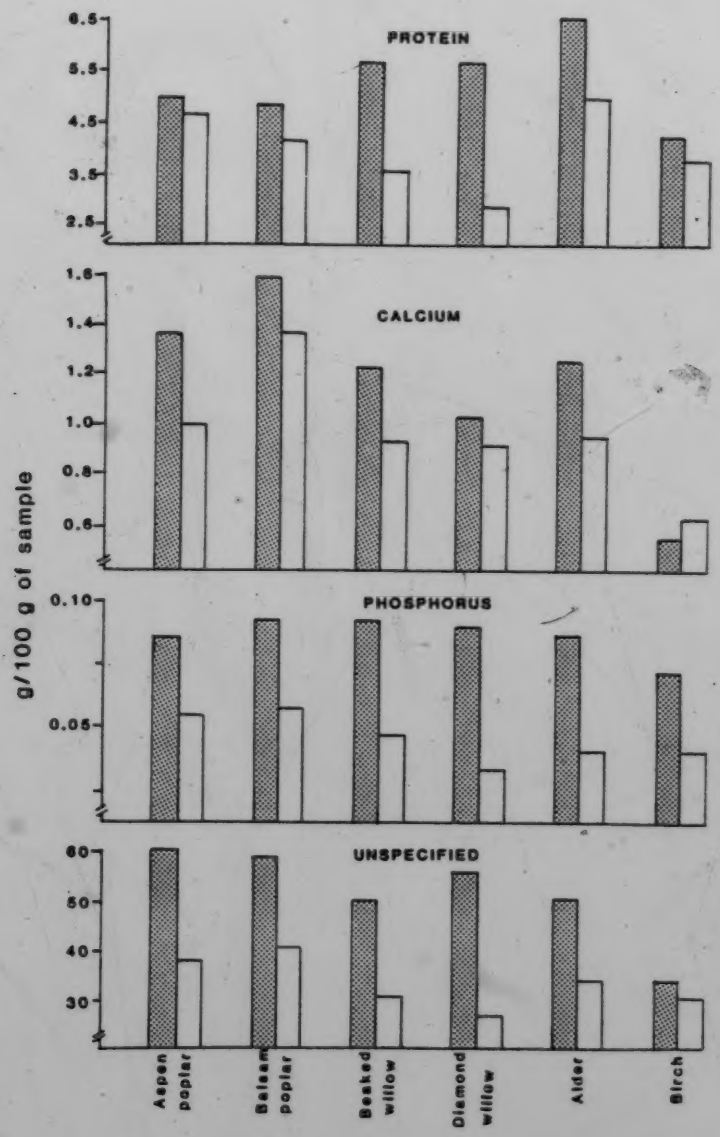

Fig. 8. Mean nutrient content of bark from six species of woody vegetation. All samples were 2 to 5 cm in diameter. The shaded bar and open bar represent levels before and after overwinter immersion, respectively.

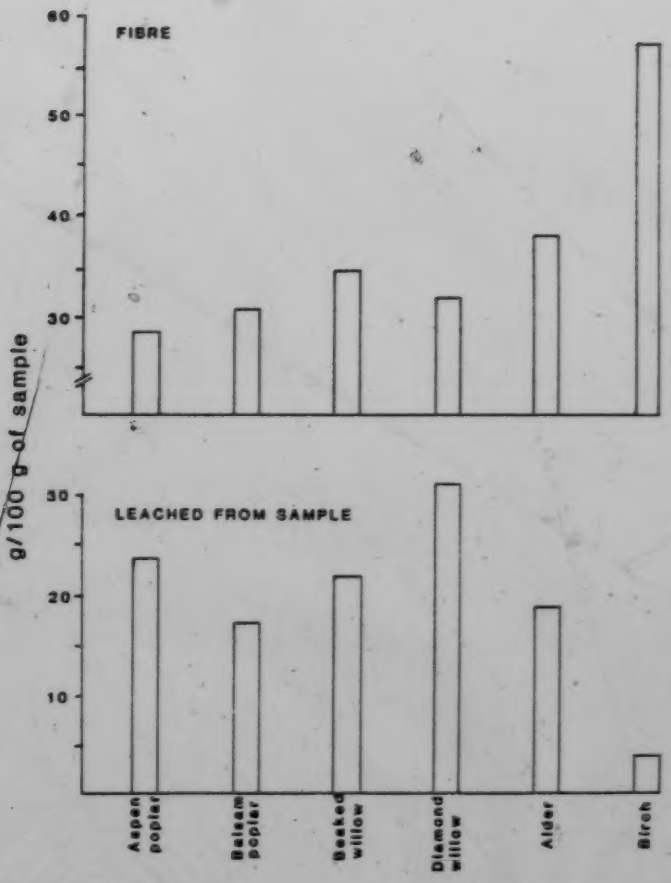

Fig. 9. Mean fibre content of bark and mean amount of material leached from the bark of food cache material from November 1982 to May 1983.

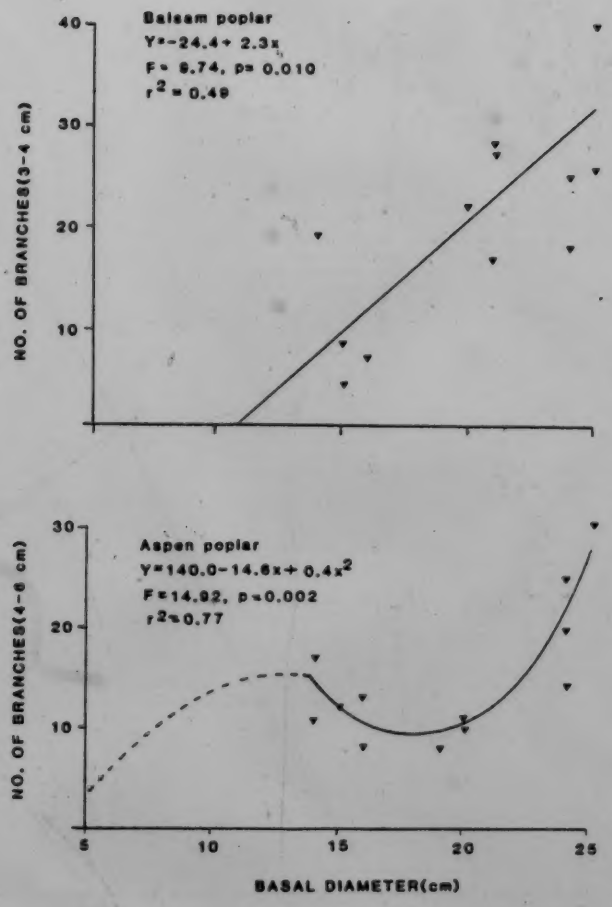

Fig. 10. Relationship of the number of branches within the size range typically used by beavers for winter food with basal diameter. The dashed line indicates values not entered into the regression analysis.

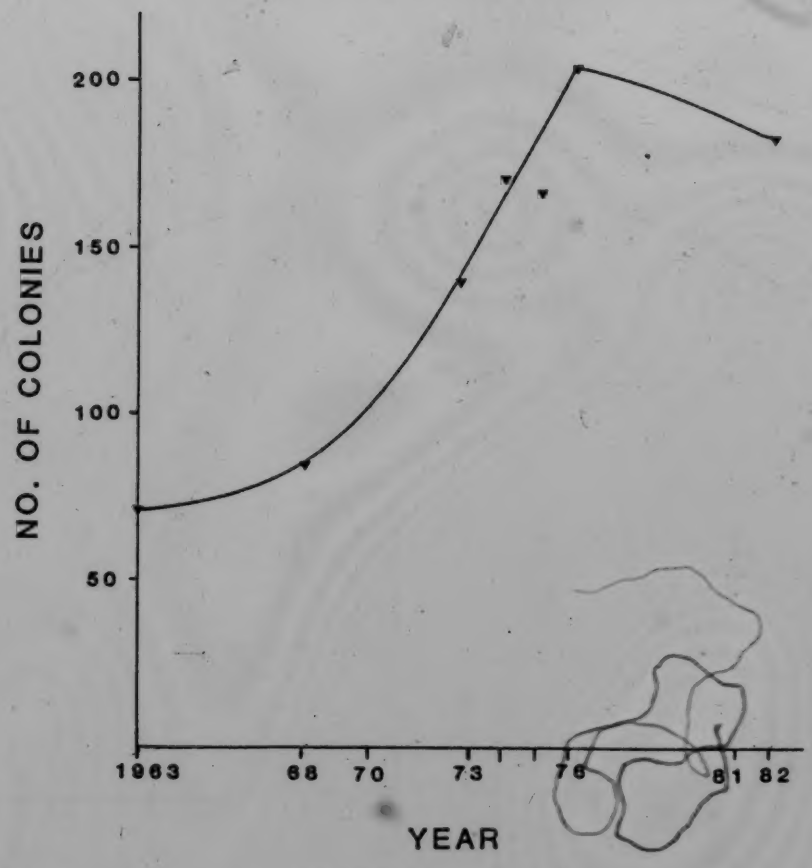

Fig. 11. Number of active colonies observed during beaver surveys of Elk Island National Park, 1963 - 1982.

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